EXAMINING SOURCES OF PRIMARY PRODUCTION AND BOTTOM-UP LIMITATIONS IN NEARSHORE ECOSYSTEMS OF THE NORTHEAST PACIFIC OCEAN USING FISH BASED INDICATORS

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Abstract

Our ability to forecast the fate of ecosystems and species hinges on an understanding of how biological systems respond to their environment. In this dissertation, natural indicators of diet (stable isotopes) and production (otolith growth increment width) in two common fishes were used to investigate energy pathways and biophysical relationships in nearshore kelp forests spanning two large marine ecosystems with contrasting oceanography, the upwelling system of the California Current and the downwelling system of the Alaska Coastal Current. Stable isotope analysis indicated high proportions of kelp-derived carbon in two common predatory fish, pelagic-feeding Black Rockfish and benthic-feeding Kelp Greenling. Routinely using both kelp and phytoplankton energy channels reflects strong benthic-pelagic coupling in nearshore marine food webs and may confer food web resilience to perturbations in either energy channel. A network of annual otolith growth chronologies were used to test bottom-up limits of production for nearshore systems and later explore other possible correlates of production. Results of hypothesis tests were consistent with bottom-up forcing of nearshore marine ecosystems, with light and nutrients constraining primary production in pelagic food webs and temperature constraining benthic food webs. A separate exploratory analysis indicated that biophysical relationships were common with (1-2 years) and without time lags and suggested that differences in the abundance and quality of prey influenced the growth of fish through bottom-up processes. The findings from the separate exploratory analysis were generally consistent with findings from hypothesis testing. Lagged relationships were consistent with increasing higher nearshore prey abundance during warm conditions in the Alaska Coastal Current and during cool conditions in the California Current in both pelagic and benthic food webs. Relationships without time lags indicated that benthic prey quality increased during warm

conditions in both current systems, while the quality of pelagic nearshore prey increased during cool conditions in the California Current and warm conditions in the Alaska Current. Overall, results of this dissertation demonstrate that kelp provides a source of energy to higher trophic level predators and that continued warming will likely have a negative influence at lower latitudes first (e.g., California Current), while production in higher latitudes (e.g., Gulf of Alaska) may initially increase.

Table of Contents

Page

Page

List of Figures

List of Tables

Page

List of Appendices

Page

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Introduction

There is an increasing need to understand biotic responses to abiotic drivers and forecast the fate of nearshore marine ecosystems, which are of high value and subject to increasing risks. Nearshore ecosystems host a disproportionately large amount of marine production, biodiversity, and services per unit surface area (Agardy et al. 2005, Harley et al. 2006, 2012, Smale et al. 2013). Nearshore areas and their adjacent continental shelves comprise only about 7% of ocean's area and 0.5% of the ocean's volume (Chen and Borges 2009), but supply 43% of the annual goods (e.g., food and materials) and services (e.g., water filtering, nutrient cycling) from the ocean (Costanza et al. 1997, Harley et al. 2006). Of these valuable coastal waters, shallow nearshore waters are the most productive. Compared to adjacent continental shelves, nearshore biomass is two orders of magnitude greater and primary production is one order of magnitude greater per unit area (Agardy et al. 2005). Risks from development and climate change are higher in nearshore systems. Nearly 40% of the global population lives within 100 km of marine coastlines, which are altered by dredging, shipping, waste disposal, aquaculture, and agricultural activities (Agardy et al. 2005). Climate warming (Cummins and Masson 2014), storm intensity (Byrnes et al. 2011), sea level rise (Harley et al. 2012), and ocean acidification (Doney et al. 2009, Koch et al. 2013) effects are likely to be observed sooner and with greater influence in nearshore systems, which have a high likelihood of experiencing multiple stressors at the intersection of marine, freshwater, terrestrial, and atmospheric realms (Adams 2005).

Kelp ecosystems are among the most productive nearshore systems and are ubiquitous along rocky, temperate shores (Steneck et al. 2002). Kelp forest habitats support a large community of invertebrates, fish, birds, and mammals, many of which are commercially important (Dayton 1985, Foster and Schiel 1985, Smale et al. 2013). Our understanding of kelp

habitats is based predominantly on research conducted at small spatial scales, within a particular bay or around a particular island. Yet, studies conducted across multiple locations that experience a range of conditions are best for discerning broad patterns and important influences.

In the northeast Pacific Ocean, two current systems with contrasting oceanography, but similar biological communities, provide a useful comparison for understanding ecosystem structure and function. The California Current is the eastern limb of the subtropical gyre and an eastern boundary upwelling current. During late spring to early fall in the California Current, seasonal northerly winds promote coastal upwelling, a process that brings cool, deep water to the coastal shelf surface and replenishes nutrients throughout the productive upwelling season (Sverdrup et al. 1942). In upwelling systems, increased pelagic production is associated with sustained upwelling and cool, salty surface waters (Chavez and Messié 2009). Upwelling winds and nutrient delivery are disrupted during El Niño atmospheric conditions and positive phases of the Pacific Decadal Oscillation with negative influences on marine fish, birds and mammals (Peterson and Schwing 2003). During late fall to early spring, southerly winds promote seasonal downwelling in the California Current.

The Alaska Coastal Current flows from the British Columbia Shelf northward and counter-clockwise around the Gulf of Alaska with cyclonic winds resulting in downwelling at the coast throughout much of the year (Royer 1998). The Alaska Coastal Current is buoyancy-driven by the difference between higher offshore marine salinities and lower nearshore salinities owing to the large amounts of freshwater discharge (Stabeno et al. 2004, Weingartner et al. 2005). Nutrient sources that support this ecosystem are varied and include a number of cross-shelf exchange mechanisms with nitrate-rich, iron-poor offshore waters replacing and mixing with nitrate-poor, iron-rich nearshore waters on the shelf (Ladd et al. 2005). Light also limits

production in this region with stratification being an important precursor to phytoplankton blooms (Henson 2007, Strom et al. 2010). In the Alaska Coastal Current and broader Gulf of Alaska, community composition varies with interannual to decadal shifts in temperature and winds associated with the strength and position of the Aleutian Low Pressure System, with some species benefitting from warmer conditions and a stronger Aleutian Low while other species benefit from cooler conditions and a weaker Aleutian Low (Anderson and Piatt 1999, Mueter and Norcross 2000, Litzow 2006).

The source of primary production and bottom-up limitations on production in kelp forest habitats in the Alaska Coastal Current and California Current are the subjects of this dissertation. I focused on two common predatory fish species that are associated with kelp habitat, Black Rockfish (*Sebastes melanops*) and Kelp Greenling (*Hexagrammos decagrammus*) (Love 2011). Black Rockfish and Kelp Greenling are widely distributed from central California to the Aleutian Islands, Alaska, USA, in the northeast Pacific Ocean with each representing one of the principal feeding modes in aquatic ecosystems, pelagic and benthic (Rosenthal 1983, Love et al. 2002, Love 2011). Black Rockfish forage pelagically on small fish and zooplankton in the water column, while Kelp Greenling forage benthically on crabs, worms, amphipods, and other invertebrates near the sea floor (Moulton 1977, Rosenthal 1983, Love 2011). The generalist feeding strategies and high trophic positions of each focal species suggest that they would be good representatives of production transferred through their respective food webs.

In this dissertation, I examined the relative importance of kelp- and phytoplankton-derived carbon using stable isotopes from fish muscle tissues and the roles of potential environmental influences on nearshore production using annual otolith growth increments in resident fish as a proxy for production. Carbon isotope values ($\delta^{13}C$) are higher in kelp than

phytoplankton and can be used to assess energy sources even when primary producers and consumers are separated by several trophic levels (Duggins et al. 1989). Fish otoliths provide a natural chronicle of individual production by recording a lifetime history of somatic body growth and condition, analogous to tree rings in terrestrial systems (Morrongiello et al. 2012, Black et al. 2013). My research focused on four broad questions: 1) Is kelp-derived carbon a common source of primary production in nearshore marine predators? (Chapter 1), 2) Are existing hypotheses relating continental shelf production to environmental influences supported in nearshore kelp forests? (Chapter 2), 3) How are basin- and local-scale environmental processes related to nearshore production? (Chapter 3), and 4) Do correlations with environmental indices suggest that new hypotheses relating nearshore fish production to the environment need to be developed? (Chapter 3).

In Chapter 1, I examined the sources of primary production for two fish species, Black Rockfish and Kelp Greenling. Primary producers fix carbon into organic material that provides energy to herbivores and ultimately all other animals in a food web. Organic carbon at our study sites was thought to be predominately derived from kelp macroalgae for benthic-feeding consumers and phytoplankton microalgae for pelagic-feeding consumers. This chapter addresses three main questions: 1) Do sources of primary production change with ontogeny (size) within each species? 2) How do sources of primary production differ between pelagic-feeding Black Rockfish and benthic-feeding Kelp Greenling?, and 3) How does the proportion of kelp-derived carbon in nearshore fish vary spatially?

In Chapter 2, I tested three hypothesized predictors of marine production to examine support for bottom-up limitations in pelagic and benthic nearshore systems using a network of annual otolith growth records from multiple sites spanning two current systems (California

Current and Alaska Coastal Current) with contrasting oceanography. Each hypothesis considered one of three potential drivers of nearshore production: summer sea surface temperature, summer upwelling, and summer phytoplankton. Each hypothesis examined bottom-up limits on growth under the assumption that pelagic nearshore food webs were nutrient limited in the California Current and light limited in the Alaska Coastal Current at the level of primary production, and benthic nearshore food webs were limited by temperature effects on benthic invertebrates or primary production in both systems.

In Chapter 3, I explored the response of nearshore production, indexed by fish growth, to basin and local-scale physical indicators. I considered the influence of basin and local-scale indicators across all seasons and with lags of up to two years to account for changes in the quantity (1-2 year time lags) and quality (within year relationships) of prey. Relationships linking fish growth to basin- (Pacific Decadal Oscillation, North Pacific Gyre Oscillation, and Multivariate ENSO Index [MEI]) and local-scale (sea surface temperature, sea surface height anomalies, upwelling, and phyotosynthetically active radiation) environmental conditions were allowed to vary by species and current system. I anticipated that nearshore pelagic rockfish would benefit from cooler conditions associated with reduced water column stability in the California Current and warmer conditions associated with strengthened water column stability in the Alaska Coastal Current, while nearshore benthic greenling would benefit from warmer conditions and strengthened water column stability in both current systems.

Chapter 1: Widespread kelp-derived carbon in pelagic and benthic nearshore fishes[1]

ABSTRACT: To explore the relative proportion of phytoplankton and kelp-derived carbon sources in nearshore marine fish predators, we measured carbon isotope values ($\delta^{13}C$) in epaxial muscle sampled from benthic-foraging kelp greenling *(Hexagrammos decagrammus)* and pelagic-foraging black rockfish *(Sebastes melanops)* at eight sites spanning ~35–60°N from the California Current (upwelling system) to the Alaska Coastal Current (downwelling system) in the northeast Pacific Ocean. Muscle $\delta^{13}C$ values were expected to be highest for fish tissue primarily derived from kelp and lower for those primarily derived from phytoplankton. The $\delta^{13}C$ values were higher in benthic-feeding kelp greenling than in pelagic-feeding black rockfish at seven of eight sites, indicating more kelp-derived carbon in greenling. The proportion of kelp-derived carbon varied by location ranging from 51-98% in kelp greenling and 54-80% in black rockfish. Kelp-derived carbon generally increased with latitude in kelp greenling and mirrored known patterns in phytoplankton availability in black rockfish, with more kelp-derived carbon in rockfish at sites with lower phytoplankton abundance. We conclude that these two nearshore fishes routinely derive carbon from kelp and phytoplankton channels across coastal upwelling and downwelling systems. This pattern of dual-channel carbon use, taken together with findings from other studies, appears to reflect a pervasive mechanism that could foster resilience of nearshore marine foodwebs to climate and human disturbances. The role of kelp in coastal marine foodwebs and the underlying mechanisms of energy and organic matter exchange deserve further attention.

1.1 Introduction

[1] von Biela, VR, Newsome, S.D., Bodkin, J.L., Kruse, G.H., and Zimmerman, C.E. Submitted. Widespread kelp-derived carbon in pelagic and benthic nearshore fish. Marine Ecology Progress Series.

Understanding stability in ecologically and economically valuable nearshore marine systems is a priority due to the increased risks of warming temperatures, rising sea levels, and human development in these ecosystems that host high amounts of biodiversity as well as economically and culturally valuable fisheries (Scavia et al. 2002, Agardy et al. 2005, Harley et al. 2006). Open ocean systems can be productive, but are inherently unstable because they are characterized by temporal and spatial fluctuations in the dominant energy source (phytoplankton), which can quickly resonate through trophic levels and may alter ecosystem function and predator biomass (Chassot et al. 2010). Predator use of multiple energy channels leads to enhanced food web stability by providing resilience to disruptions in the production of any particular channel (McCann et al. 2005, Rooney et al. 2006, Haddad et al. 2011). When predators use multiple energy channels, the result of declining aGbvailability in any one source may be balanced by continued availability of another source, particularly when production in one energy channel is quick and another is slow (Rooney et al. 2006). Fast channels have higher production:biomass ratios driven by stronger food web interactions that more efficiently move energy through food webs as compared to slow channels (Rooney et al. 2006). Pelagic food webs that rely on phytoplankton are fast channels, while benthic food webs that rely on macroalgae are slow channels. Fishes integrate both fast phytoplankton and slow algae channels in lacustrine ecosystems (Vander Zanden and Vadeboncoeur 2002) and nearshore marine fish may also use energy from multiple channels, namely phytoplankton and macroalgae.

Nearshore marine predators can obtain energy that is derived from phytoplankton, macroalgae (e.g., kelp and seagrass), and terrestrial primary producers (Duggins et al. 1989, Fredriksen 2003, Tallis 2009, Dunton et al. 2012, von Biela et al. 2013). Use of multiple energy channels, however, has not been broadly examined for nearshore ecosystems containing both

kelp and phytoplankton based primary production; we define nearshore marine ecosystems in this study as subtidal rocky reefs characterized by canopy and understory forming kelp (brown algae of the order Laminariales) in the neritic zone. Use of kelp carbon could be particularly widespread and important given its global distribution in temperate and sub-arctic nearshore systems (Dayton 1985, Estes and Steinberg 1988). In nearshore rocky reefs, kelp food webs are a slow energy channel and phytoplankton food webs are a fast energy channel with spatial and seasonal differences in the availability of each energy source (Duggins et al. 1989, Lindstrom 2009). If predators in nearshore food webs routinely combine contributions from both kelp and phytoplankton, the resilience of ecosystem function in the face of natural and/or anthropogenic stressors could be higher than if predators used only one source of primary production.

Past food web studies in nearshore ecosystems have described the importance of kelp carbon to primary consumers, but few studies have identified kelp carbon contributions to predators. Low trophic level benthic invertebrates have been shown to directly consume kelp (kelp herbivores, e.g. urchins) or kelp detritus (filter and suspension feeders, e.g. clams and mussels) (Duggins et al. 1989, Eckman and Duggins 1991, Fredriksen 2003, Salomon et al. 2008, Tallis 2009). Benthic-foraging nearshore predators such as sea otters (*Enhydra lutris*; (Estes et al. 2003, Laidre and Jameson 2006, Newsome et al. 2009), Atlantic cod (*Gadus morhua*; Steneck et al. 2002), and California sheephead (*Semicossyphus pulcher*; Hamilton et al. 2011, 2014) rely on these benthic invertebrates, providing a likely pathway from kelp to benthic predators. The few studies that have demonstrated high proportions of kelp-derived carbon in predators (Duggins et al. 1989, McMeans et al. 2013, Hamilton et al. 2014), have considered only benthic predators at a single study site. If the use of multiple energy channels is important

to nearshore food web stability, kelp- and phytoplankton- derived carbon should be present in both benthic and pelagic predators across many locations.

Carbon can be traced through food webs by analyzing carbon isotope values ($\delta^{13}C$) in the tissues of consumers from multiple trophic levels. Kelp isotope ratios are higher than those of phytoplankton and these differences propagate up the food chain even when predators are separated from primary producers by several trophic levels (Duggins et al. 1989, Fredriksen 2003, Page et al. 2008, Michener and Kaufman 2007, Tallis 2009). When the isotope values of both primary producers (e.g., kelp and phytoplankton) and focal consumers (e.g., fish) are directly measured, a stable isotope mixing model can estimate the relative contribution of each primary producer (Parnell et al. 2010). Mixing models also require estimates of consumer trophic level and trophic discrimination factors, defined as the isotopic difference between consumer tissues and that of their prey ($\Delta^{13}C_{tissue\text{-}diet}$).

Black rockfish and kelp greenling are ideal focal predators for examining the use of both kelp and phytoplankton-derived carbon channels in the northeast Pacific Ocean. Both species are widely distributed in nearshore habitats with small individual home ranges (~ 1 km^2; Parker et al. 2007, Love 2011), assuring that capture locations reflect foraging grounds. Each species represents one of the two principal feeding modes in aquatic marine ecosystems, benthic and pelagic. Black rockfish are water-column generalists that consume forage fish, euphausiids, and zooplankton, often aggregating near steep rocky reefs in relatively shallow water <55m deep (Rosenthal 1983, Brodeur et al. 1987, Love et al. 2002, Love 2011, Pirtle et al. 2012). Kelp greenling are benthic generalists that consume sea cucumbers, brittle stars, crabs, amphipods, shrimp, worms, and snails on or near the sea floor (Moulton 1977, Rosenthal 1983, Love 2011). We anticipated that each species would derive carbon from both kelp and phytoplankton

channels, but that black rockfish would derive more carbon from phytoplankton than do kelp greenling. Ontogenetic dietary shifts may occur in either species, thus we considered individual fish size prior to making comparisons among sites. To determine whether pelagic and benthic-feeding predators consistently use both kelp and phytoplankton carbon channels, black rockfish and kelp greenling were collected from eight sites in the northeast Pacific Ocean from California to Alaska, spanning 25 degrees of latitude (~35 to 60°N) and two large marine ecosystems, the California Current and Gulf of Alaska. The former is a seasonal coastal upwelling system, whereas the latter is predominantly a year-round downwelling system.

1.2 Methods

1.2.1 Sample collection and stable isotope analysis

A total of 308 black rockfish and 336 kelp greenling were captured at eight subtidal rocky reef sites in the northeast Pacific Ocean: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); and Big Sur, CA (BIGS) (Figure 1.1; Table 1.1). Sea otters were present at all sites; predation by otters increases kelp production and species diversity via top-down control of major kelp grazers such as sea urchins (*Strongylocentrotus spp.*; Estes & Duggins 1995, Steneck et al. 2002, Watson & Estes 2011). Fish were collected using trammel nets, hook and line sampling, or spear fishing in 2010 and 2011 (Table 1.1). Most collections occurred between April and September, but some samples were collected in October from WASH (n=12) and November from MONT (n=7). Collection month was not standardized as it is unlikely to influence isotope ratios, because muscle tissue of slow-growing adult fish (age: 1+) living in cold waters likely has a slow isotopic incorporation rate and probably reflects from several months up to one year of

foraging information (Hesslein et al. 1993, Perga and Gerdeaux 2005, Weidel et al. 2011). Epaxial muscle was sampled and stored frozen prior to stable isotope analysis.

Epaxial muscle samples were freeze-dried and subsampled for stable isotope analysis at the University of Wyoming Stable Isotope Facility (Laramie, WY). Each sample was analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values using a NC 2500 Carlo-Erba or a Costech 4010 Elemental analyzer (Costech Analytical, Valencia, CA) interfaced with a Thermo-Finnigan Delta Plus XP continuous-flow stable isotope ratio mass spectrometer (Thermo Electron Corp., Waltham, MA). Stable isotope values are reported using standard delta notation, $\delta^{15}N$ or $\delta^{13}C = 1000\ [(R_{sam}/R_{std})-1]$, where R_{sam} and R_{std} are the $^{15}N:^{14}N$ or $^{13}C:^{12}C$ ratios of the sample and standard, respectively. Lipids were not extracted prior to analysis because the mean (±SD) ratio of carbon:nitrogen concentration, expressed as [C]/[N] ratios, of fish muscle for both species was 3.2±0.1, which is indicative of pure protein containing negligible lipid content (Sotiropoulos et al. 2004, Ricca et al. 2007, Post et al. 2007, Logan et al. 2008). The within-run standard deviation of $\delta^{13}C$ and $\delta^{15}N$ reference materials, calibrated to internationally accepted Vienna-Pee Dee Belemnite (V-PDB) and atmospheric N_2, was ≤0.2‰.

1.2.2 Statistics and stable isotope mixing models

A set of linear mixed-effect models was used to test the influence of fish length on $\delta^{13}C$ for each species. In the full model, $\delta^{13}C$ is described by length (X_i) and random site effects for the intercept and slope:

$$\delta^{13}C_{ki} = (\alpha + a_k) + (\beta + b_k)X_i + \varepsilon_{ki}\ , \qquad (1.1)$$

where $\delta^{13}C_{ki}$ is the carbon isotope value of fish *i* from site *k* and is estimated by a fixed intercept α, a random site-specific deviation that allows average isotope levels to differ among sites a_k, a fixed length effect β, and a site specific deviation in the length effect b_k that allows

the effect of length on isotope values to vary across sites. The random effects a_k and b_k are assumed to follow a bivariate normal distribution with mean 0, variances σ_a and σ_a and covariance σ_{ab}. Residuals are assumed to be independent of the random effects and normally distributed such that:

$$\varepsilon_{ki} \sim N(0, \sigma^2)$$

The full model was compared to nested models without random length effects ($b_k = 0$ for all k) and without fixed or random length effects ($\beta = b_k = 0$) using paired likelihood ratio tests. Random site-specific intercepts were included in all models to account for known shifts in isotopic baselines across wide geographic scales. Isotopic baseline shifts are differences in the isotope values of primary producers that vary spatially with a host of physical and chemical variables (Casey and Post 2011). Carbon source between black rockfish and kelp greenling were compared at each site with independent two-sample t-tests of $\delta^{13}C$ that assumed unequal variance following Leven's test. Comparisons of $\delta^{13}C$ between greenling and rockfish at each site require several common assumptions, including similar (1) trophic levels, (2) trophic discrimination factors between species, and (3) end-member values so that differences in $\delta^{13}C$ are primarily reflecting differences in carbon source and not a result of standardization (Duggins et al. 1989, Fredriksen 2003, Miller et al. 2008).

Comparisons across sites required the use of site-specific isotope mixing models to account for differences in kelp and phytoplankton $\delta^{13}C$ and $\delta^{13}N$ values at each location. $\delta^{13}C$ and $\delta^{15}N$ values from kelp and phytoplankton were based on literature that reported mean isotope values and associated standard deviation at a nearby location (Table 1.2). Phytoplankton isotope values were measured from samples of particulate organic matter (POM) suspended in the water column 100 m to 3 km offshore (Table 1.1). End member values were not available for sites in southeast Alaska, so values from the northern Gulf of Alaska were applied. Little shift in

baseline isotope values was anticipated between these localities based on a lack of consistent geographic pattern in weathervane scallop (*Patinopecten caurinus*) isotope values from the northern to eastern Gulf of Alaska (Andrews 2010). Kelp isotope end-member values were based on the dominant kelp species at each site: *Macrocystis pyrifera* at sites in California, Washington, and British Columbia (Tallis 2009, Foley and Koch 2010, Markel 2011) and *Nereocystis luetkeana* in Alaska (Dean et al. 2000, Lindstrom 2009). Fresh kelp samples were used to estimate the kelp end-member value, but the majority of kelp-derived carbon may enter these food webs as detritus (Krumhansl and Scheibling 2012). Stable isotope values are fairly robust to decomposition and minimal influence on isotope values was assumed (Fenton and Ritz 1988, Kaehler et al. 2006, Schaal et al. 2009). Other kelp species (e.g., *Saccharina* and *Agarum*) exist at our Alaska study sites and have similar isotope values as the dominant species used in our analysis (Dethier et al. 2013).

Trophic discrimination factors of 0.5‰ and 3.4‰ per trophic level were assumed for $\delta^{13}C$ and $\delta^{15}N$, respectively (Vander Zanden and Rasmussen 2001, Post 2002, McCutchan et al. 2003). Trophic level (TL) was calculated based on differences in $\delta^{15}N$ between primary producers and fish at each site following Post (2002):

$$TL = 1 + (\delta^{15}N_{fish} - [\delta^{15}N_{phytoplankton} x\, \alpha + \delta^{15}N_{kelp} x(1-\alpha)])/\Delta^{15}N \quad (1.2)$$

In this equation, $\Delta^{15}N$ is the nitrogen discrimination factor and α is the proportion of phytoplankton derived carbon. For the trophic level calculation, α was set at 0.5, but estimates should not be sensitive to this assumption, as $\delta^{15}N$ values are similar for kelp and phytoplankton producers relative to the 3.4‰ enrichment per trophic level. Bayesian mixing models were constructed using package SIAR (Parnell et al. 2010) in R (R Core Team 2013) statistical software for all sites except MONT. The SIAR model inputs included the means and standard

deviations of $\delta^{15}N$ and $\delta^{13}C$ for phytoplankton and kelp end members, trophic enrichment factors multiplied by the estimated mean trophic level of fish at each site, a standard deviation for the trophic enrichment factors, as well as the $\delta^{15}N$ and $\delta^{13}C$ values for individual fish of each species at each site. No prior information on the mean proportions for each dietary source or elemental concentration data was included in the model. The SIAR package fits models using Markov Chain Monte Carlo (MCMC) simulations. Mixing models were not implemented for fish captured at MONT, as most isotope values for individual fish fell outside the mean of the phytoplankton and kelp end members. When consumers' isotope values fall outside the end-member values, it is likely that sources of primary production have been poorly defined and, as a result, mixing models return nonsensical results (Phillips and Koch 2002).

The program SIAR allowed errors in discrimination factors and carbon sources (i.e., kelp and phytoplankton) to propagate through the mixing model and provide a more accurate measure of uncertainty. Incorporating error provides a buffer against known seasonal, interannual, and spatial variation in $\delta^{13}C$ of primary producers and uncertainty in discrimination factors (Simenstad et al. 1993, Page et al. 2008, Bond and Diamond 2011, Miller and Page 2012, Fox 2013). The standard deviation of discrimination factors was set at 0.5‰ for both $\delta^{15}N$ and $\delta^{13}C$ based on literature values (McCutchan et al. 2003, Bond and Diamond 2011). The model does not consider other possible carbon sources, such as terrestrial plants, non-kelp macroalgae (e.g., green and red macroalgae) or seagrasses. The possibility of terrestrial carbon sources at these sites was minimal due to limited riverine influence and selection for habitats on exposed coastlines. Similarly, we observed kelps dominating the macroalgal biomass in the subtidal habitats and an expected lack of seagrass beds along the exposed coastlines sampled in our study (seagrass beds did occur in the protected bays). In response to recent studies that indicate

Bayesian mixing models are highly sensitivity to discrimination factors (Bond and Diamond 2011) and the possibility that $\delta^{13}C$ discrimination factor ($\Delta^{13}C$) can be much higher, we also considered an alternative mixing model where $\Delta^{13}C$ was 1.0‰ per trophic level (Dubois et al. 2007, Kilham et al. 2009, Elsdon et al. 2010), rather than 0.5‰. Both scenarios are plausible and are considered in the discussion.

1.3 Results

A model with a fixed fish length effect improved predictions of $\delta^{13}C$ in black rockfish (likelihood ratio test $P = 0.02$, Table 1.3), but random fish length effects for each site did not result in additional improvement ($P = 0.39$). The average length of black rockfish sampled differed among sites with several pairwise differences among sites; one-way ANOVA, F =3.57, $P < 0.001$. Rockfish from BIGS and MONT were the smallest and those from ELFI and WPWS were largest, while other sites were intermediate in mean length. Values of $\delta^{13}C$ increased by ~0.3‰ over the observed length range of ~200-500mm. As this difference is within the error of $\delta^{13}C$ discrimination factors, it was not considered in comparisons among sites and species. For kelp greenling, fixed and random fish length effects did not improve model fit (Table 1.3). Within site variance in $\delta^{13}C$ between species was unequal at 4 of 8 sites (MONT, WASH, WHAL, ELFI) based on Levene's test ($P < 0.05$). Kelp greenling $\delta^{13}C$ were significantly higher compared to black rockfish at all sites except BIGS; t-tests with unequal variances, $P < 0.001$ (Figure 1.2). At BIGS, kelp greenling and black rockfish had similar $\delta^{13}C$ ($P = 0.06$).

Fish were estimated to be 2.2 to 2.6 trophic levels above primary producers based on the difference between fish and primary producer $\delta^{15}N$ values. The proportion of kelp-derived carbon estimated from mixing models varied across sites (Figure 1.3). The mean (±SD) proportion of kelp carbon in rockfish captured at sites in Alaska was ~75-80% (WHAL, 80 ±3%;

ELFI, 75±3%; WPWS, 81±3%; KATM, 81±3%) while the mean proportion of kelp carbon in fish captured from southern locations ranged more widely from 69±6% at BIGS, 48±3% at WASH, and 54±1% at CLAY (Figure 1.3a). Kelp greenling captured at northern sites contained more kelp-derived carbon than those from southern sites with fish from BIGS (63±8%) and WASH (51±3%) using the least kelp carbon, fish from CLAY (71±1%), WHAL (78±3%), and ELFI (72±3%) indicating intermediate kelp-derived carbon, and fish from WPWS (83±2%) and KATM (99±1%) having the highest proportion of kelp-derived carbon (Figure 1.3b). When mixing model assumptions were modified by doubling $\Delta^{13}C$ from 0.5‰ to 1.0‰, mean (±SD) estimates of kelp carbon use were reduced by 17±3%. On average, the proportion of kelp carbon in fish was ~70% when using a $\Delta^{13}C$ of 0.5‰ and 55% when $\Delta^{13}C$ was doubled to 1‰.

1.4 Discussion

This study is the first to demonstrate widespread kelp-derived carbon in nearshore fish and suggests that kelp energy channels may extend to marine birds and mammals that consume nearshore fish. Our findings highlight the occurrence of strong pelagic-benthic coupling in nearshore waters (Kopp et al. 2015). The use of two energy channels has previously been associated with increased food web stability and resilience in both aquatic and terrestrial ecosystems (McCann et al. 2005, Rooney et al. 2006, Haddad et al. 2011). Kelp beds have been known to benefit fish by providing habitat (Bodkin 1986, Holbrook et al. 1990, Reisewitz et al. 2006, Siddon et al. 2008, Efird & Konar 2014), and our isotopic evidence suggests that kelp also provides an important source of primary production for the food webs of benthic-feeding kelp greenling and pelagic-feed black rockfish. Depending on mixing model assumptions, our data show that kelp carbon contributed an average of 55-70% of carbon to the muscle tissue of nearshore fish across sites and species. Our results are consistent with previous isotope studies

that have documented similarly high contributions of kelp carbon to nearshore predators at single localities, including 40-70% kelp carbon in body tissue of rock greenling, predatory sea stars, and cormorants at sites in the Aleutian Islands (Duggins et al. 1989), 40-70% kelp carbon in fish and birds in a Norwegian kelp forest (Fredriksen 2003), 40-70% kelp carbon in epibenthic fishes in an Antarctic kelp forest (Dunton 2001), 60-65% kelp carbon in black and copper rockfish off Vancouver Island (Markel 2011), and 50% kelp carbon in predatory snails in the Beaufort Sea (Dunton and Schell 1987).

1.4.1 Change in $\delta^{13}C$ with fish length

Fish length had a surprisingly weak effect on $\delta^{13}C$ with small increases in larger black rockfish and no effect for kelp greenling. The difference between species may reflect differences in diet with size or where these species occur during their early life. Black rockfish in nearshore habitats consume fewer zooplankton and more fish as they grow larger (Love 2011) and ontogenetic shifts in diet could cause a shift in carbon source if forage fish (e.g., herring) have higher carbon isotope values as compared to zooplankton. Alternatively, black rockfish have a prolonged offshore pelagic life stage lasting 3 to 6 mo before settlement in nearshore systems, while kelp greenling complete all life history phases in nearshore habitats (Love et al. 2002, Love 2011, Lotterhos and Markel 2012). During this offshore pelagic phase, juvenile (age-0) black rockfish likely rely on offshore phytoplankton-based food webs associated with lower $\delta^{13}C$ values (Miller et al. 2008; von Biela et al. 2015). The observed increase in $\delta^{13}C$ with size in black rockfish, but not kelp greenling, is consistent with continued replacement and dilution of carbon obtained during early life in offshore habitats with that from nearshore kelp-dominated habitats.

The influence of fish length on $\delta^{13}C$ also had a very small effect on $\delta^{13}C$ across sites. While $\delta^{13}C$ values increased with black rockfish size, which varied among sites, the increase in $\delta^{13}C$ with length was small (~0.3‰) relative to the uncertainty in the end-member values and trophic discrimination factors used in the mixing models. Differences in average length among sites may also reflect differences in effort among sampling gear (trammel net, hook and line, and spear) used to collect fish and may not necessarily be representative of the mean size of the fish populations present at each location. Nevertheless, observed differences in isotope values across sites cannot be explained by differences in fish length.

1.4.2 Differences in $\delta^{13}C$ between black rockfish and kelp greenling

Kelp greenling tissue was composed of more kelp-derived carbon than black rockfish at all but one site (Figure 1.2). Kelp greenling feed primarily on benthic invertebrates that may derive >50% of their carbon from kelp (Duggins et al. 1989, Eckman and Duggins 1991, Fredriksen 2003, Salomon et al. 2008, Tallis 2009) and thus provide a trophic link between kelp and benthic fish predators. Lower proportions of kelp-derived carbon in black rockfish is consistent with a tendency to feed on zooplankton and forage fish in the water column, which are thought to derive more carbon from phytoplankton-based food webs (Kline 1999, Miller et al. 2008). Big Sur was the only site where the proportions of rockfish and greenling kelp carbon sources were similar. This site has low phytoplankton concentrations all year long as persistent upwelling and offshore advection of surface currents drives phytoplankton blooms offshore (Foley 2009), perhaps resulting in a higher reliance by rockfish on kelp-derived carbon in the nearshore pelagic food web.

1.4.3 Differences in kelp versus phytoplankton-derived carbon use among sites

Our mixing models suggest widespread kelp-derived carbon in both fish species across sites under either set of mixing model assumptions: $\delta^{13}C$ trophic discrimination factor of 0.5‰ or 1.0‰ per trophic level (Figure 1.3). While the proportion of kelp-derived carbon was reduced when the trophic discrimination factor was doubled for each trophic level separating fish from primary producers, the results of both model scenarios were similar and our interpretations considered both scenarios jointly. Kelp-derived carbon in kelp greenling was moderate to high (40-100%) with greater kelp carbon at more northern sites (Figure 1.3). High proportions of kelp-derived carbon in kelp greenling was not surprising given their reliance on benthic prey and strong isotopic evidence of kelp carbon use among a variety of benthic invertebrates (Moulton 1977, Duggins et al. 1989, Fredriksen 2003, Salomon et al. 2008, Tallis 2009, Love 2011). Increasing proportions of kelp-derived carbon in kelp greenling with latitude loosely follows shifts in canopy kelp species composition and an increase in understory kelps. *Macrocystis* dominates at southern sites with limited understory kelp and *Nereocystis* dominates at northern sites with abundant understory kelp (Bodkin 1986, Dean et al. 2000, Foley 2009, Lindstrom 2009, Tallis 2009, Markel 2011). As a perennial species, *Macrocystis* provides a more continuous source of kelp production to nearshore marine communities throughout the year, while annual *Nereocystis* and associated understory decomposition in the late summer and fall at northern sites could provide a large pulse of high quality kelp detritus to consumers during a time of diminishing phytoplankton availability (Duggins et al. 1989).

Among black rockfish, models suggest moderate to high proportions of kelp-derived carbon, similar to kelp greenling (Figure 1.3). Similar proportions of kelp-derived carbon in black rockfish and kelp greenling is surprising, as black rockfish are often assumed to be strongly linked to phytoplankton food webs through their zooplankton and forage fish prey

(Kline 1999, Miller et al. 2008), and our results raise questions about how kelp-derived carbon reaches black rockfish. The possibility that pelagic organisms may assimilate kelp detritus is a relatively recent suggestion based on the observation that kelp detritus can be entrained in the water column as a component of suspended particulate organic matter (SPOM; Kaehler et al. 2006, Hill et al. 2008) and thus become available to pelagic consumers like zooplankton. Indeed, recent within-species comparisons of individuals captured along an onshore to offshore gradient indicated that individuals captured closer to shore contained more benthic carbon (Kopp et al. 2015). For instance, Atlantic herring (*Clupea harengus*) primarily relied on pelagic carbon in offshore habitats and benthic carbon nearshore habitats (Kopp et al. 2015).

Alternatively, high proportions of kelp-derived carbon in black rockfish may reflect a higher reliance on benthic prey by black rockfish or the forage fish consumed by black rockfish. Black rockfish (Hallacher and Roberts 1985, Brodeur et al. 1987) and the forage fish species consumed by black rockfish (Moulton 1977, Rosenthal 1983, Hallacher and Roberts 1985, Brodeur et al. 1987) opportunistically consume benthic prey (e.g., polychaetes and mysids), especially when pelagic prey are less abundant. Still, black rockfish feeding morphology (e.g., small mouth, long intestines, and long gill rakers) is more consistent with pelagic foraging in the water column (Hallacher and Roberts 1985) and supports the assumption that the benthos is not their primary foraging habitat (Love 2011). Because benthic feeding is relatively infrequent for black rockfish and the forage fish they predate, it is likely that kelp detritus contributes to pelagic food webs as a component of SPOM and becomes available to black rockfish.

The proportion of kelp-derived carbon in rockfish varied by site and mirrored the pattern in regional phytoplankton abundance. While phytoplankton abundance varies widely in the coastal northeast Pacific Ocean, annually integrated chlorophyll concentrations in Washington

and southern British Columbia are twice that found in the other two regions sampled in this study: central California and the Gulf of Alaska (Ware and Thomson 2005). Proportionately more phytoplankton and less kelp-derived carbon occurred in rockfish at sites associated with higher phytoplankton abundance (WASH and CLAY), compared to other study sites. The association between phytoplankton abundance and carbon contribution suggests that phytoplankton is a preferred carbon pathway for black rockfish.

Differences in the seasonal availability of phytoplankton and kelp-derived carbon (Duggins et al. 1989, Foley 2009) may explain why both carbon sources are widely used by nearshore fishes and coastal food webs more generally. Phytoplankton abundance is highest during the spring and summer months when both nutrients and light are available for pelagic primary producers, while kelp-derived carbon availability is thought to be highest in the winter due to senescing annual species (e.g., *Nereocystis*) or storm damage to perennial species (e.g., *Macrocystis*) (Duggins et al. 1989). Indeed, kelp contributions to filter-feeding mussels and barnacles tend to be higher during winter months when kelp detritus is likely more available than phytoplankton carbon in some locations (Foley 2009, Tallis 2009).

Some studies have dismissed the widespread use of kelp-derived carbon in marine systems based on low nutritional quality or biased phytoplankton end-members (Page et al. 2008, Miller and Page 2012). The nutritional quality of kelp has been assessed by the concentration of defensive compounds, such as polyphenolics, as well as carbon and nitrogen concentrations, often reported as C/N ratios (Duggins and Eckman 1997, Norderhaug et al. 2003). The nutritional quality of kelp tissue increases as it ages via reduction of defensive compounds and increasing nitrogen concentration (lower C/N ratios) as evidenced by improved growth rates of consumers that forage on this food source (Duggins and Eckman 1997). Defensive compounds

can be high in some kelps, but kelps in the North Pacific Ocean generally have low concentrations of defensive compounds and are thought to have evolved during a time when benthic predators maintained top-down control of herbivores, making defensive compounds, that are energetically costly to synthesize, unnecessary (Estes and Steinberg 1988).

The end member isotope value for phytoplankton can often be biased if collected too far offshore due to differences in species composition, dissolved inorganic carbon concentration, and phytoplankton growth rates (Miller and Page 2012). Miller and Page (2012) suggested that studies of nearshore communities revealing dependence on kelp-derived carbon have been consistently biased, because researchers tend to use $\delta^{13}C$ values from offshore phytoplankton that was collected 10s to 100s of kilometers from nearshore sites. In our study, the phytoplankton end member was represented by POM collected in coastal locations just 100 m to 3 km from shore to provide a more realistic representation of phytoplankton available to nearshore consumers. This approach risks contamination from kelp detritus in the form of SPOM, but reduces overestimation of kelp-derived carbon. If our POM end members were routinely contaminated by enriched kelp detritus, it would cause an enrichment bias. An enrichment bias in the depleted end member shrinks the expected range of consumer isotope values and can shift the depleted end member, phytoplankton, closer to the consumer values and result in a systematic underestimation of kelp-derived carbon.

Kelp end members were based on isotope values for the dominant canopy forming kelp species at each study site (*Nereocystis* at sites in Alaska and *Macrocystis* other sites), but the proportions of kelp-derived carbon described in this study may include other enriched carbon sources with similar isotope values. Microphytobenthos (unicellular algae and cyanobacteria in the top layer of sediment) and other kelp species (e.g., *Saccharina*) tend to have similar isotopic

composition (Sokołowski et al. 2012, Dethier et al. 2013), making distinction difficult using bulk isotope analysis. Both microphytobenthos and other kelp species can be important sources of primary production for consumers (Duggins et al. 1989, MacIntyre et al. 1996, Fredriksen 2003, Takai et al. 2004). Yet, along rocky shores with abundant kelp, such as those sampled in this study, kelp production likely dominates over microphytobenthos production (Dalsgaard 2003) since rocky substrates are associated with sparse microphytobenthos (Paterson and Hagerthey 2001). Given the dominance of kelp and rocky substrates at our study sites, the contribution of ^{13}C-enriched microphytobenthos to the food web is likely to be small.

Reliance on kelp energy channels deserves further investigation with more refined techniques, such as amino and fatty acid $\delta^{13}C$ analysis, to more accurately resolve patterns in carbon sources (Dethier et al. 2013, Larsen et al. 2013). Additional techniques can help address the uncertainty in trophic discrimination factors and primary producer end member values and possibly better partition sources of primary production among microphytobenthos, multiple species of macroalgae, and phytoplankton. Nevertheless, our results suggest that kelp is an important component of nearshore food webs and provides another reason to consider protection and conservation of kelp habitats in management plans. While these communities may have some food web resilience, they are also facing multiple stressors including warming, ocean acidification and fishing (Agardy et al. 2005, Harley et al. 2012).

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Table 1.1. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of black rockfish (*Sebastes melanops*) and kelp greenling (*Hexagrammos decagrammus*) collected from rocky nearshore habitats throughout the northeast Pacific Ocean.

Site	Site Code	Collection Dates	Species	N	$\delta^{13}C \pm SD$	$\delta^{15}N \pm SD$	Length ± SD (mm)
Katmai National Park, south central Alaska	KATM	July 2010	*S. melanops*	39	-17.3 ± 0.5	14.3 ± 0.5	404 ± 99
			H. decagrammus	47	-15.8 ± 0.5	14.6 ± 0.5	272 ± 80
Western Prince William Sound, south central Alaska	WPWS	June and August 2010	*S. melanops*	38	-17.7 ± 0.6	14.9 ± 0.5	471 ± 70
			H. decagrammus	82	-16.8 ± 0.5	14.5 ± 0.6	278 ±85
Elfin Cove, Chichagof Island, southeast Alaska	ELFI	May 2011	*S. melanops*	45	-18.0 ± 0.3	14.0 ± 0.5	440 ± 44
			H. decagrammus	41	-17.3 ± 0.7	14.4 ± 0.5	323 ± 45
Whale Bay, Baranof Island, southeast Alaska	WHAL	May and June 2011	*S. melanops*	44	-17.6 ± 0.3	13.7 ± 0.4	384 ± 44
			H. decagrammus	41	-17.1 ± 0.6	14.6 ± 0.5	317 ± 36
Clayoquot Sound, Vancouver Island	CLAY	May 2010 and July 2011	*S. melanops*	55	-16.2 ± 0.4	14.9 ± 0.4	424 ± 37
			H. decagrammus	53	-15.3 ± 0.4	15.5 ± 0.4	316 ± 63
Neah Bay, Olympic Peninsula, Washington	WASH	2010 and 2011	*S. melanops*	49	-16.6 ± 0.4	14.9 ± 0.7	384 ± 55
			H. decagrammus	38	-16.0 ± 0.7	14.6 ± 0.7	386 ±27
Monterey Bay, central California	MONT	September and November 2010	*S. melanops*	13	-16.4 ± 0.3	14.9 ± 0.6	270 ± 51
			H. decagrammus	17	-14.9 ± 0.4	15.8 ± 0.7	324 ± 77
Big Sur, central California	BIGS	September 2010	*S. melanops*	25	-16.5 ± 0.6	14.5 ± 0.5	278 ± 50
			H. decagrammus	17	-16.1 ± 0.7	15.2 ± 0.2	340 ± 27

Table 1.2. Kelp and phytoplankton carbon and nitrogen end members used in mixing models. Phytoplankton was represented by suspended particulate organic matter (POM) in the water column. Sites are abbreviated as follows: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); Big Sur, CA (BIGS).

	KELP			PHYTOPLANKTON		
Site	$\delta^{13}C$ (±SD)	$\delta^{15}N$ (±SD)	Source	$\delta^{13}C$ (±SD)	$\delta^{15}N$ (±SD)	Source
KATM	-17.6 ± 1.0	7.4 ± 1.3	*Nereocystis* from Takli Island and Kaflia Bay, KATM (n = 20)	-23.0 ± 1.8	6.5 ± 1.2	Mean POM values collected ~100m offshore at sites in Katmai and Kenai Fjords National Parks, and western Prince William Sound (n = 11).
WPWS	-17.5 ± 1.0	7.5 ± 1.9	*Nereocystis* from Johnson Bay, WPWS (n = 10)			
ELFI			Used WPWS end members			
WHAL						
CLAY	-14.8 ± 0.2	6.5 ± 0.3	*Macrocystis* collected between Kyuquot Sound and Nuchatlitz Inlet (n = 44, Markel 2011)	-20.3 ± 0.9	6.9 ± 0.9	marine POM collected 100-250m offshore (n = 44, Markel 2011)
WASH	-13.7 ± 0.3	6.1 ± 3.0	Mixed kelp detritus from Olympic Peninsula sites (n =2, Tallis 2009)	-20.2 ± 3.2	6.7 ± 3.2	Summer marine POM collected at river plume edges (n = 46, Tallis 2009)
MONT	-17.8 ± 3.5	7.3 ± 1.2	Pre-experiment mature *Macrocystis* blades (n = 29, Fox 2013)	-22.8 ± 1.9	5.1 ± 0.7	Summer marine POM collected 3km offshore Big Sur coastline (n = 6, Foley 2009)
BIGS	-17.5 ± 3.0	6.7 ± 1.9	*Macrocystis* from Big Sur coastline (n = 238, Foley 2009)	-22.8 ± 1.9	5.1 ± 0.7	Summer marine POM collected 3km offshore Big Sur coastline (n = 6, Foley 2009)

Table 1.3. Model selection results for predicting black rockfish (n=308) and kelp greenling (n=336) carbon isotope values using individual fish length as a fixed or random site effect. Models in italics provided the best fit for each model group as judged by AIC values.

Model	**df**	**ΔAIC**
Black rockfish		
Fixed length effect	*4*	*0*
Fixed and random length effects	6	2.1
No length effect	3	3.0
Kelp greenling		
No length effect	*3*	*0*
Fixed length effect	4	1.2
Fixed and random length effects	6	4.9

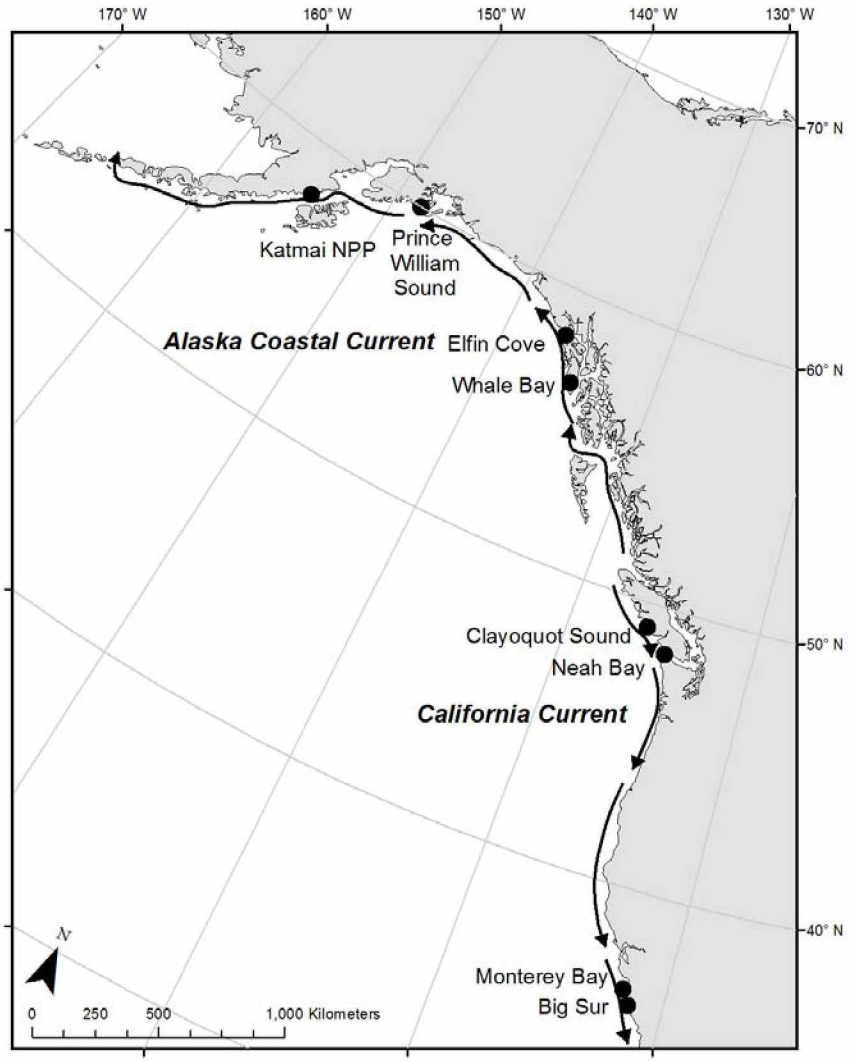

Figure 1.1. Nearshore fish collection sites (solid dots) and generalized nearshore current flow in summer (arrows) in the Alaska Coastal Current and California Current.

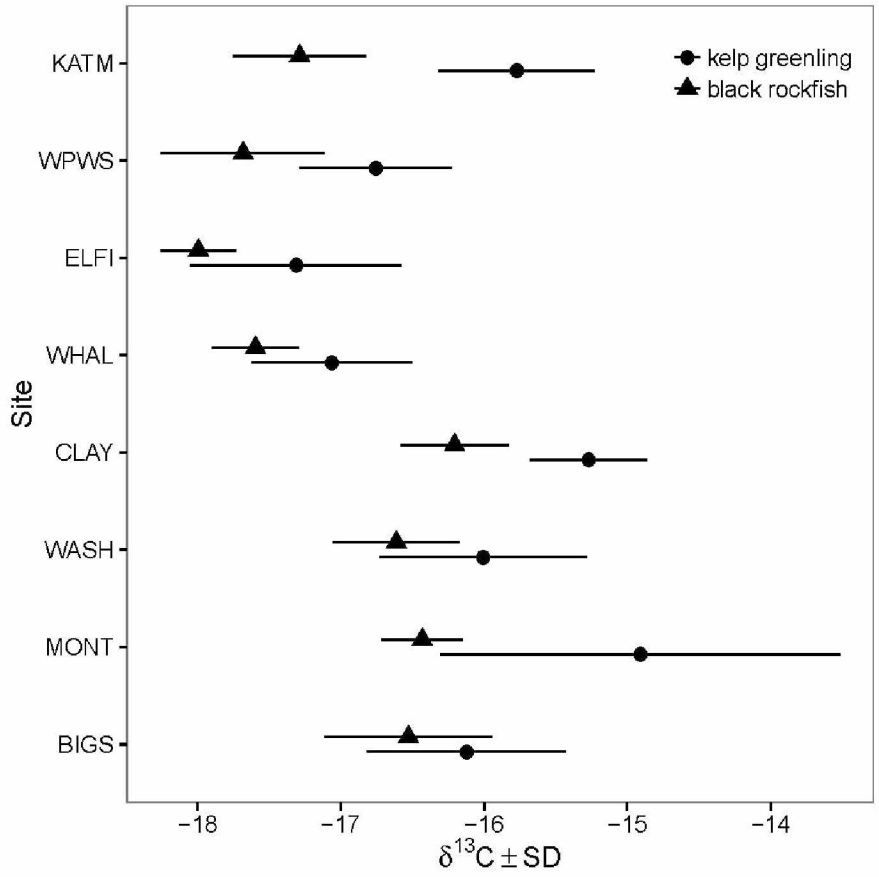

Figure 1.2. Mean (±SD) carbon (δ13C) isotope values of kelp greenling (circles) or black rockfish (triangles) muscle from each study site. Sites are ordered geographically from north (top) to south (bottom) of the figure. Within each site, higher δ13C values indicate more kelp carbon use. Sites are abbreviated as follows: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); Big Sur, CA (BIGS).

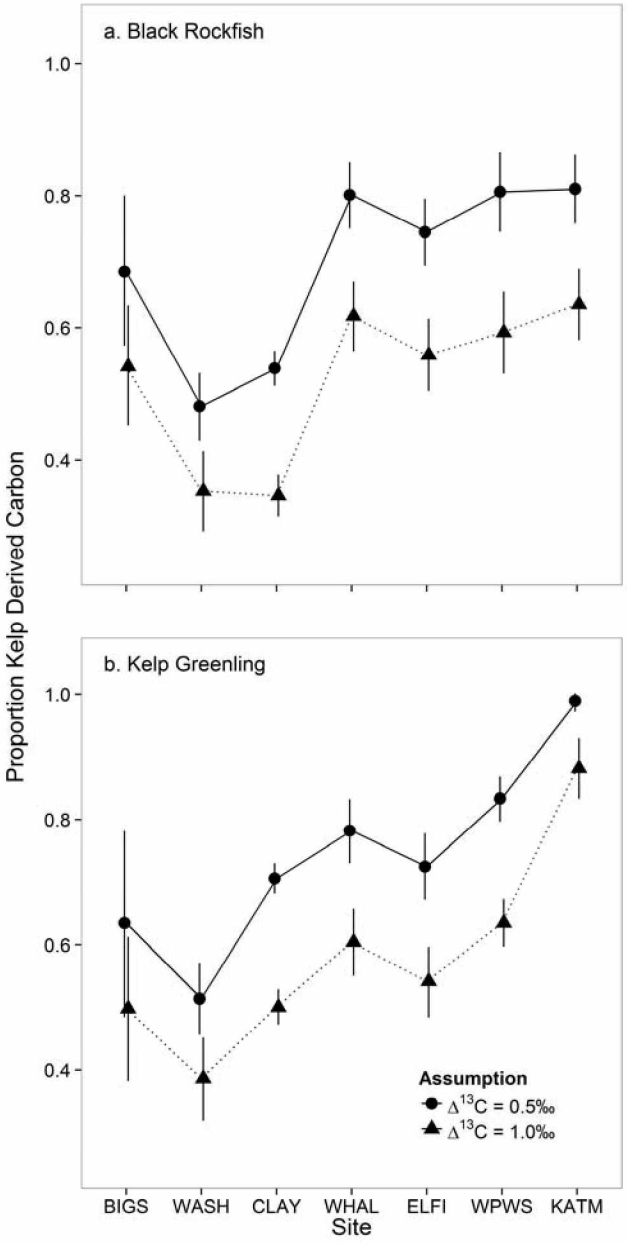

Figure 1.3. Kelp carbon assimilation estimated by mixing models for black rockfish (a) and kelp greenling (b); error bars represent 95% confidence intervals. Both models use the same site-specific end members for phytoplankton and kelp (Table 2) and assume a trophic discrimination factor of 3.4‰ per trophic level for δ15N. Trophic discrimination factor (Δ13C) differ by model assuming either a 0.5‰ (circles with solid line) or 1.0‰ (triangles with dotted line) increase per trophic level. The standard deviation of Δ13C was 0.5‰ under both assumptions. Sites are abbreviated as follows: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); Big Sur, CA (BIGS).

1.7 Appendices

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2 messages

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Hi Seth,

I need your permission to include the following paper in my dissertation:

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Thanks!

Vanessa

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Seth Newsome <newsome@unm.edu> Thu, Jan 8, 2015 at 2:48 PM
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Hi Vanessa...

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Seth

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Appendix 1.1. Permission to use manuscript in dissertation from Seth Newsome

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Appendix 1.2. Permission to use manuscript in dissertation from James Bodkin

Chapter 2: Evidence of bottom-up limitations in nearshore marine systems based on otolith proxies of fish growth[1]

Abstract

Fish otolith growth increments were used as indices of annual production at nine nearshore sites within the Alaska Coastal Current (downwelling region) and California Current (upwelling region) systems (~36-60°N). Black rockfish (*Sebastes melanops*) and kelp greenling (*Hexagrammos decagrammus*) were identified as useful indicators in pelagic and benthic nearshore food webs, respectively. To examine support for bottom-up limitations, common oceanographic indices of production (sea surface temperature [SST], upwelling, and chlorophyll-*a* concentration) during summer (April-September) were compared to spatial and temporal differences in fish growth using linear mixed models. Pelagic black rockfish exhibit a positive growth relationship with SST in the cooler Alaska Coastal Current and a negative relationship in the warmer California Current. These contrasting growth responses to SST among current systems are consistent with the optimal stability window hypothesis in which pelagic production is maximized at intermediate levels of water column stability. Increased growth rates of black rockfish were associated with higher chlorophyll concentrations in the California Current only, but black rockfish growth was unrelated to an index of upwelling strength in either current system. Benthic kelp greenling growth rates were positively associated with warmer temperatures and relaxation of downwelling in the Alaska Coastal Current, while none of the oceanographic indices were related to their growth in the California Current. Overall, our results

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[1] von Biela, V.R., Kruse, G.H., Mueter, F.J., Black, B.A., Douglas, D.C., Helser, T.E., and Zimmerman C.E. 2015. Evidence of bottom-up limitations in nearshore marine systems based on otolith proxies of fish growth. Marine Biology. doi: 10.1007/s00227-015-2645-5

are consistent with bottom-up forcing of nearshore marine ecosystems – light and nutrients constrain primary production in pelagic foodwebs, and temperature constrains benthic foodwebs.

2.1 Introduction

Nearshore systems (defined here to be within 1 km of shore) are among the world's most productive marine habitats, supporting a diversity of fish, bird, and mammal populations. However, relatively little is known about the bottom-up oceanographic conditions that influence production, impeding the ability to predict future conditions under various climate regimes or global warming scenarios (Agardy et al. 2005, Harley et al. 2006). In nearshore systems, top-down competition and trophic cascades have long been identified as important ecosystem controls. More recent studies have considered bottom-up oceanographic influence on population recruitment and community structure through larval delivery (reviewed in Menge 2000) and determined that food limitation can be common in nearshore systems (Cloern and Jassby 2008). Bottom-up controls may have received less attention because nearshore systems are "green" with abundant photosynthetic biomass, which suggests the generally accepted importance of top-down control by herbivores (Hairston et al. 1960, Steneck et al. 2002). Temperate kelp forests are particularly productive nearshore systems, producing ~2.5 kg m^{-2} y^{-1} of biomass compared to only ~0.36 kg m^{-2} y^{-1} of biomass in adjacent continental shelves (hereafter referred to as offshore) (Agardy et al. 2005) largely due to the combined primary production by benthic macroalgae and water column phytoplankton (Duggins et al. 1989). High primary production sustains more consumers and provides important foraging areas for a variety of resident and nonresident species (Duggins et al. 1989). Nonresident species often use nearshore systems during critical life history phases (e.g., reproduction and juvenile growth), highlighting the

importance of this system to marine populations beyond the nearshore (Kruse and Tyler 1989, Dean et al. 2000, Laurel et al. 2007, Doyle et al. 2009).

While production is consistently higher in nearshore compared to offshore regions, nearshore systems are characterized by high interannual and spatial variability owing to a large number of environmental influences from terrestrial and marine sources (Harley et al. 2006, Cavanaugh et al. 2011). In offshore marine habitats, several climate-based hypotheses have been developed to explain causes of interannual variation in production and to anticipate future changes, but few of these mechanisms have been tested or developed for nearshore systems (Hoegh-Guldberg and Bruno 2010). Bottom-up drivers in offshore systems may influence nearshore systems if nutrients or plankton are advected onshore (Steneck et al. 2002, Barth et al. 2007, McPhee-Shaw et al. 2011). A significant limitation to establishing such climate-biology relationships is that many years of biological data across multiple sites are needed, but relatively few long-term annual datasets exist for nearshore resident species. Fish otoliths, however, provide a natural chronicle of individual production by recording a lifetime history of body growth and condition, analogous to tree rings in terrestrial systems (Morrongiello et al. 2012, Black et al. 2013).

To understand oceanographic influences on nearshore systems, we developed a network of otolith growth records from multiple sites spanning two current systems with contrasting oceanography, and then we compared fish growth response to spatial and temporal variation in sea surface temperature (SST), upwelling, and chlorophyll concentrations. Contrasts between upwelling and downwelling regions have increased our understanding of oceanographic drivers of production along continental shelves (Ware and McFarlane 1989, Brodeur et al. 1996, Gargett 1997, Black et al. 2008). Along the western coasts of northern continents, coastal upwelling is

the ocean response to equatorward winds driving a net offshore movement of surface waters, while downwelling is the response to poleward winds driving onshore movement of surface waters. Both phenomena exert strong influences on vertical stratification, cross-shelf exchange, and nutrient distribution (Huyer 1983). The northeast Pacific Ocean continental shelf encompasses the California Current upwelling and Alaska Coastal Current downwelling systems (Ware and McFarlane 1989) (Figure 2.1).

Sea surface temperature, upwelling, and chlorophyll concentrations are good predictors of marine production and biomass at higher trophic levels in offshore pelagic systems (Ware and Thomson 2005, Behrenfeld et al. 2006, Mueter et al. 2009, Demarcq 2009). These environmental indicators are routinely monitored and reflect ecosystem processes that are otherwise difficult to measure. For example, sea surface temperature often reflects water column stability (Boyce et al. 2010). In upwelling systems, cooler SST indicates strong vertical mixing and availability of deep water nutrient sources (Sydeman and Allen 1999, Chavez and Messié 2009, Demarcq 2009, Black et al. 2011) while further north in the Gulf of Alaska, warm SST reflects seasonal increases in water column stability and solar radiation that support photosynthesis (Mueter et al. 2009, Strom et al. 2010, Boyce et al. 2010). Primary production may be maximized at intermediate levels of water column stability with sufficient mixing to replenish nutrients and enough stratification to retain phytoplankton in the photic zone (Sverdrup et al. 1942, Gargett 1997). Coastal upwelling indices are correlates for large-scale vertical mixing of deeper, nutrient-rich water that promotes production in nutrient-limited systems, or hinders production in light-limited systems that benefit from increased stratification (Barth et al. 2007, Demarcq 2009, Takahashi et al. 2012). Satellite-based chlorophyll-*a* indices approximate phytoplankton standing stock biomass available to aquatic food webs; higher values of

chlorophyll-*a* have been associated with increased fish catches (Ware and Thomson 2005, Boyce et al. 2010).

Production in benthic systems has also been associated with SST, upwelling, and chlorophyll (Menge et al. 1997, Steneck et al. 2002, Blanchette et al. 2006, 2007, Broitman et al. 2008). Surface temperature can be used as an indicator of benthic temperature conditions in shallow-water (<12 m deep) nearshore habitats where tidal currents and wave action mix the water column from top to bottom (Smale and Wernberg 2009). In contrast to patterns found in pelagic systems, reduced upwelling and warmer temperatures in nearshore habitats tend to be associated with increased benthic invertebrate production; these relationships are consistent across upwelling and downwelling regions (Phillips 2005, Blanchette et al. 2006). Warmer water present during downwelling or relaxed upwelling conditions may be indicative of increases in invertebrate larval recruitment associated with onshore advection or delivery of zooplankton or detritus to the benthic invertebrate communities (Phillips 2005, Blanchette et al. 2006). Growth rates of benthic consumers have been linked to chlorophyll concentrations in some (Menge et al. 1997) but not all cases examined (Phillips 2005, Blanchette et al. 2006).

Ideal indicator species for nearshore production are non-migratory, nearshore resident species with generalist diets that can be caught easily throughout a wide geographic range (Morrongiello et al. 2012). Black rockfish (*Sebastes melanops*) and kelp greenling (*Hexagrammos decagrammus*) were identified for this study as useful indicator species feeding in pelagic and benthic nearshore food webs, respectively. Both species are nearshore residents with similar geographic ranges, small individual home ranges, and association with rocky reef kelp communities (Parker et al. 2007, Freiwald 2009, Love 2011, Green and Starr 2011). Fish with small home ranges provide a record of local production near their capture location. Black

rockfish feed in the water column on forage fish including Pacific herring (*Clupea pallasi*), sand lance (*Ammodytes hexapterus*), and juvenile salmon (*Oncorhynchus spp.)*, and invertebrates, such as crab megalopae (Love et al. 2002, Love 2011, Sturdevant et al. 2012). Kelp greenling are benthic generalists, foraging on a variety of benthic invertebrates including: snails, sea cucumbers, decorator crabs, and brittle stars (Moulton 1977, Love 2011). Both species are widely distributed from the Aleutian Islands to central California (Love 2011), spanning the Alaska Coastal Current and California Current and thus allowing comparisons between downwelling and upwelling current systems.

In this study, hypothesized oceanographic predictors of marine production (SST, upwelling, and chlorophyll concentrations) in pelagic and benthic nearshore systems were tested using black rockfish and kelp greenling otolith growth increment widths. As these hypotheses involve environmental conditions in the current year of growth and our focal species tend to consume prey $\geq$1 year old, changing environmental conditions likely influence nearshore fish by controlling the quality, rather than the abundance, of their prey. The body condition of key prey groups (forage fish and invertebrates) is already known to respond quickly (within the year) to environmental conditions (Astthorsson and Gislason 1998, Robards et al. 2002, Phillips 2005, Blanchette et al. 2006, MacFarlane 2010, Takahashi et al. 2012). We examined the following bottom-up hypotheses for the pelagic nearshore using black rockfish: (H_1) fish growth is positively associated with cooler summer temperatures in the California Current and warmer summer temperatures in the Alaska Coastal Current; (H_2) fish growth is positively associated with upwelling in the California Current system and fish growth is negatively associated with downwelling in the Alaska Coastal Current system; and (H_3) fish growth in both current systems is positively associated with local summer chlorophyll concentrations. Benthic nearshore (i.e.,

kelp greenling) hypotheses are that: (H_4) fish growth is positively associated with warmer temperatures in both systems; (H_5) fish growth is positively associated with relaxation of upwelling in the California Current and downwelling in the Alaska Current systems; and (H_6) fish growth is positively associated with local increases in summer chlorophyll concentrations. Each hypothesis examines bottom-up limits on growth under the assumption that pelagic nearshore food webs are nutrient limited in the California Current and light limited in the Alaska Coastal Current at the level of primary production, and benthic nearshore food webs are limited by temperature effects on benthic invertebrates or primary production.

2.2 Methods

Nearshore production was indexed using the annual growth increments recorded in black rockfish and kelp greenling otoliths collected at nine sites in the California Current and Alaska Coastal Current (Table 2.1, Figure 2.1). All fish were captured within study site boundaries determined *a priori* based on habitat characteristics. Study sites were characterized by rocky reef habitat, and the presence of macrophytes (kelp), and sea otters *(Enhydra lutris)*, a keystone predator in nearshore systems known to increase community diversity and kelp production via top-down control of major kelp grazers such as sea urchins (*Strongylocentrotus spp.*; Steneck et al. 2002). Fish were captured using trammel nets, spearfishing, and hook and line sampling in shallow nearshore waters (<5 m depth).

Otoliths were embedded in epoxy and sectioned through the nucleus on a transverse plane using a low-speed wafering saw to allow for measurements of annual growth increments on a thin section approximately 0.5 mm wide (Black et al. 2008). Measurements of each annual growth increment, delineated from the interior edge of an opaque zone to the outer edge of the next translucent zone, were made along a line perpendicular to the axis of growth on a high

resolution image captured with a digital camera (Leica DFC 425 or 450) mounted on a stereomicroscope (Leica MZ6 or M60) under 20x to 40x magnification using ImagePro Plus 7.0 software (Media Cybernetics, Rockville, MD, USA) following Black et al. (2005). The first growth increment was not included given that it represents age-0 growth when habitat and diet differ from later ages (Love et al. 2002, Love 2011, Lotterhos and Markel 2012) nor was the last increment given that it is incomplete at the time of capture. The calendar year of each increment formation was assigned by working backwards from the year of capture at the outer most growth increment.

Each series of growth increments from a given location were crossdated to ensure accuracy in year assignment following methods of Black et al. (2005). Crossdating is principally a visual procedure, and was statistically verified using the computer program COFECHA (http://web.utk.edu/~grissino/software.htm). In COFECHA, long-term trends, including age-related growth declines, were removed and the growth pattern of each individual was correlated with the average of all others. A low correlation is an indicator that an error may have occurred. In such case, the sample was visually re-inspected to identify any missed or falsely added increments. At no time was crossdating "forced" on any individual; changes were made to measurements only if there was clear visual evidence that an error had been made. The annual periodicity of increment formation, and thus accuracy of black rockfish age assignments, is supported by anomalous oxygen stable isotope values in otoliths associated with the 1983 El Niño event (Piner et al. 2005) and bomb radio carbon dating (K. Munk, Alaska Dep. of Fish and Game, pers. comm.). Kelp greenling otolith age has been validated with oxytetracycline marks in the otoliths of captive fish (S. Hoobler, Calif. Dept. of Fish and Wildlife, pers. comm.). Using otolith growth increments as proxies for fish growth is supported by strong positive correlations

between otolith and somatic size in black rockfish (Munk 2012) and kelp greenling (this study; fork length in mm vs. otolith radius measured from the focus to the ventral proximal edge on the longest axis in microns of 50 randomly selected individuals; slope = 2.4; $r^2 = 0.75$, $P < 0.05$). To establish a series of growth increments from an individual for cross-dating, only fish 5 yr and older at capture were included in this study (age range 5 to 40 yr old) and the increments measured spanned the sub-adult and adult growth history (increments representing age-1 growth and beyond).

Monthly SST and chlorophyll-*a* data, gridded over 4-km resolution, and monthly coastal upwelling indices were used to predict annual growth. Monthly mean values were averaged over a 6 mo summer period, April-September (Menge and Menge 2013). Summer averages were chosen to integrate conditions across the growing season in an effort to match the season of opaque zone, the larger component of an annual increment in otoliths of northern hemisphere fish (Beckman and Wilson 1995). Monthly SST averages were extracted from AVHRR PathFinder version 5.0 satellite SST data for each site from 1982 to the year prior to collection (http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/userguide.html). For SST, the study site area included a 100 km buffer (buffered site area in Table 2.1) to increase the number of grid cells sampled (878 to 4079 pixels) and site area (range 14,000 to 60,000 km^2). In all cases, the spatial extent of an SST calculation was truncated at the 200 m isobath. We made no attempt to interpolate missing data, which represented 13% of pixels in an average month. At all sites, chlorophyll-*a* concentrations (mg/m^3) were available from MODIS-Aqua satellite data with 4-km resolution from 2003 to the year prior to collection (May 2012 release, http://oceancolor.gsfc.nasa.gov/). For chlorophyll analyses, study sites did not include a 100 km buffer because the possibility of patchy chlorophyll distributions make localized data more

desirable, even at the expense of reducing the number of grid cells sampled (62 to 279 pixels). On average, 12% of pixels had missing chlorophyll data. Upwelling indices were obtained from the Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/) for the latitude and longitude closest to each study area and for all years with increment growth data. When an entire month of data for an environmental variable was missing, the site and year was dropped from the analysis.

Hypotheses relating annual growth to summer conditions were tested using linear mixed models to account for intrinsic (age or size) and extrinsic (environmental) growth components using the 'nlme' package in the statistical program R (Weisberg et al. 2010, Morrongiello et al. 2011, R Development Core Team 2013). All models included age during increment formation as an intrinsic component to account for faster growth when fish are young (Morrongiello et al. 2011). Annual otolith increment widths and age were log-transformed prior to analysis to achieve homoscedasticity and a linear relationship between these two variables. Growth intercepts (increment width at age-0) for individual fish were included as random effects nested within a random site effect, in addition to an overall model intercept across all sites. Black rockfish models also included random slope terms for the fixed age effect that modify the effect of age on growth for individual fish nested within sites, essentially fitting an individual growth trajectory to each fish and site. In doing so, the model varies the relationship between age and increment width around the site-specific mean slope. Models predicting kelp greenling annual growth increments did not converge when random slopes were included for each individual, so only random intercepts were included. Random intercepts and slopes provide a means of detrending age-related growth for each individual, similar to techniques that have traditionally been used in dendrochronology studies. Including site as a random intercept and slope effect

allows for local site-specific deviations from the overall model intercept and slope. Models independently considered the extrinsic influence of SST, upwelling, or chlorophyll concentration as fixed effects. Only one extrinsic influence was considered at a time so that all available data could be used, rather than truncating all models to data with the shortest time series.

Models were formulated to allow the relationships between annual otolith growth increments (μm y^{-1}) and summer SST, upwelling, or chlorophyll to vary by current system. The width of an annual increment in year *t*, at site *k*, for individual *i* is y_{tki} and was estimated as:

$$y_{tki} = (\alpha + a_k + a'_{i(k)}) + (\beta + b_k + b'_{i(k)})X_{ti} + \gamma_c SST_{tk} + \varepsilon_{tki}\,, \qquad (2.1)$$

where α is the fixed intercept, and a_k and $a'_{i(k)}$ are the random deviations in the intercept for each site, *k*, and individual, *i*, nested within sites, respectively. Similarly, the decline in growth with age (X_{ti}) is described by a fixed slope, β, a random site deviation, b_k, and an individual deviation $b'_{i(k)}$. The growth response to SST (SST_{tk}) in year *t* differed by current system as a fixed effect (γ_c). The variance-covariance structure of the random effects is given by:

$$\boldsymbol{b_k} = \begin{bmatrix} a_k \\ b_k \end{bmatrix} \sim N(0, \boldsymbol{\Psi_1}) \qquad \boldsymbol{b_{i(k)}} = \begin{bmatrix} a'_{i(k)} \\ b'_{i(k)} \end{bmatrix} \sim N(0, \boldsymbol{\Psi_2}),$$

where $\boldsymbol{b_k}$ is the site level random effects vector, assumed to be independent for different *k*, $\boldsymbol{b_{i(k)}}$ is the individual within site-level random effects vector, assumed to be independent for different *i*, *k* and independent of the $\boldsymbol{b_k}$, and $\boldsymbol{\Psi_1}$ and $\boldsymbol{\Psi_2}$ are unstructured 2x2 variance-covariance matrices. The errors ε_{tki} are assumed to be first-order autocorrelated within individuals and independent of the random effects, such that:

$$\varepsilon_{tki} = \phi \cdot \varepsilon_{t-1,ki} + \nu_t \qquad \text{and} \qquad \nu_t \sim N(0, \sigma_\nu^2)\,,$$

where ϕ is the first-order autoregressive coefficient and ν_t is a normally distributed variable with mean 0 and variance σ_ν^2. Autocorrelation was included to capture time series patterns in growth

anomalies that could not be explained by the selected covariates. Upwelling, UW_{tk}, or chlorophyll concentrations, $Chla_{tk}$, were considered in lieu of SST by substituting these terms for SST_{tk} in eq (1).

As an alternative model for black rockfish, a dome-shaped influence of SST on growth was included through a quadratic SST term that was assumed to capture SST effects across both current systems:

$$y_{tki} = \left(\alpha + a_k + a'_{i(k)}\right) + \left(\beta + b_k + b'_{i(k)}\right)X_{ti} + \gamma_1 SST_{tk} + \gamma_2 SST_{tk}^2 + \varepsilon_{tki} . \qquad (2.2)$$

Such a continuous, dome-shaped relationship would likely indicate that temperature is directly influencing growth via its effect on metabolic rate. If the relationship between temperature and growth is discontinuous across oceanographic domains as modeled in Equation 2.1, then that may suggest that temperature is indirectly influencing growth via impacts on lower-trophic production.

The kelp greenling global model without random slope effects for age was:

$$y_{tki} = \left(\alpha + a_k + a'_{i(k)}\right) + \beta X_{ti} + \gamma_c SST_{tk} + \varepsilon_{tki}. \qquad (2.3)$$

As with black rockfish, UW_{tk} and $Chla_{tk}$ were substituted for SST_{tk} when appropriate, to test their effects on growth increments.

An alternative model for a dome-shaped influence of SST on kelp greenling growth was also included to consider evidence for a direct effect of temperature on growth:

$$y_{tki} = \left(\alpha + a_k + a'_{i(k)}\right) + \beta X_{ti} + \gamma_1 SST_{tk} + \gamma_2 SST_{tk}^2 + \varepsilon_{tki} . \qquad (2.4)$$

Models were initially fitted using maximum likelihood for model comparisons, with the best model refitted using restricted maximum likelihood to obtain unbiased coefficients (Pinheiro

and Bates 2000). Nested model formulations with and without each environmental effect were compared using the Akaike Information Criterion to determine the best fit (Burnham and Anderson 2001). Individual coefficients were evaluated using a statistical significance level of $P < 0.05$ and depicted using output from the 'effects' package in R (R Development Core Team 2013). Multicollinearity among SST, upwelling, and chlorophyll was examined within each site using linear regression.

2.3 Results

Black rockfish from the Alaska Coastal Current yielded records spanning the 1980s through the 2000s (Figure 2.2). Black rockfish from the California Current and kelp greenling provided annual otolith growth increments primarily during 2000-2010 only because of the younger ages of capture compared to those in the Alaska Coastal Current (Figure 2.2). For both species, increment sample sizes were largest in the 2000s. Correlations between individual time series of detrended annual growth increments and the average of all others (the series intercorrelation, as provided by COFECHA) were comparable with values from other studies (Black et al. 2005) (Table 2.2).

Mixed models supported hypotheses relating SST to black rockfish and kelp greenling growth. Inclusion of current-specific SST effects improved models of annual black rockfish and kelp greenling growth compared to SST models with either a quadratic effect, a single linear effect applied to both current systems, or no effect (Table 2.3). Pelagic black rockfish growth was faster with warmer SST in the Alaska Coastal Current (Figure 2.3a, $P = 0.0003$ for SST coefficient) and cooler SST in the California Current (Figure 2.3b, $P = 0.01$ for SST coefficient). Kelp greenling growth increased with warmer SST in the Alaska Coastal Current (Figure 2.4a, $P = 0.0004$) and had a similar, albeit non-statistically significant, relationships with SST in the

California Current (Figure 2.4b, $P = 0.1$). Because SST-growth models with discontinuous linear effects by current systems (Eq. (2.1) and Eq. (2.3)) yielded better fits than the models with a continuous quadratic effect across current systems (Eq. (2.2) and Eq. (2.4)), we *a posteriori* examined black rockfish and kelp greenling models with a discontinuous quadratic effect for each current system (i.e., separate dome-shaped relationships in each current system) to verify that model improvement was not related to the inclusion of current system. We found that a discontinuous quadratic effect of SST on growth was not supported over the discontinuous linear effects for either species.

Inclusion of upwelling or chlorophyll concentration did not consistently improve models of black rockfish and kelp greenling growth. Upwelling was related to the growth of kelp greenling, but not black rockfish (Table 2.3, Figure 2.3c, $P = 1.0$; and 3d, $P = 0.08$). Relaxed summer downwelling was associated with improved kelp greenling growth in the Alaska Coastal Current (Figure 2.4c, $P= 0.0003$), but no relationship was observed between upwelling and kelp greenling growth in the California Current (Figure 2.4d, $P = 0.3$). Chlorophyll concentrations improved annual growth predictions for black rockfish, but not kelp greenling (Table 2.3). Black rockfish grew faster during years of higher summer chlorophyll concentration in the California Current (Figure 2.3f, $P = 0.006$); a similar trend was present in the Alaska Coastal Current (Figure 2.3e, $P = 0.07$). Kelp greenling growth was not related to chlorophyll in the California (Figure 2.4e, $P = 0.3$) or Alaska Coastal Currents (Figure 2.4f, $P = 0.4$). Multicollinearity was weak among environmental variables at each site (Table 2.4).

2.4 Discussion

The relationship of black rockfish growth to SST and chlorophyll concentrations provides some evidence of coherence with offshore pelagic systems in support for our hypotheses. Black

rockfish growth increased with SST in the Alaska Coastal Current, decreased with SST in the California Current, and increased with chlorophyll concentrations. The kelp greenling growth response was related to SST and upwelling also in support of our hypotheses, but not chlorophyll concentrations. Kelp greenling growth rates were positively associated with warmer temperatures and relaxation of downwelling in the Alaska Coastal Current. Overall, SST was the most consistent predictor of growth across nearshore pelagic and benthic food webs and current systems in our study. It should be noted, however, that longer data records were available for SST (28 years) and upwelling (39 years), compared to chlorophyll concentrations (8 years) and the difference in time series length could have influenced the general finding that SST was the most consistent predictor of growth. Interseries correlations of black rockfish and kelp greenling otolith growth records were comparable to other studies and indicate synchrony among individuals as well as accurate age assignments and growth increment delineation (Black et al. 2005, 2008, 2009).

2.4.1 Sea surface temperature

Our findings that pelagic black rockfish growth is positively related to SST in the Alaska Coastal Current and negatively related to SST in the California Current are consistent with the optimal stability window hypothesis developed for continental shelf ecosystems. The optimal stability window hypothesis suggests production peaks with intermediate water column stability, which allows some mixing for nutrient replenishment but enough stratification to keep plankton in the photic zone (Gargett 1997). Nearshore primary producers (phytoplankton and macrophytes) also acquire nutrients from deep water sources through mixing and cross-shelf exchange mechanisms (Steneck et al. 2002, Hickey and Banas 2003, Ladd et al. 2005) and can be light limited (Steneck et al. 2002, Hickey and Banas 2003, Etherington et al. 2007,

Kavanaugh et al. 2009). Gargett (1997) used SST as a stability proxy in the California Current and discharge as a stability proxy in the Alaska Coastal Current, as seawater densities are primarily controlled by temperature and salinity in these two systems, respectively. Here, SST was used as a proxy for water column stability in both the Alaska Coastal Current and California Current, because spatially explicit salinity or discharge data were unavailable across the study range and SST has been used as an indication of water column stability in other Pacific Ocean studies (Thomas et al. 2012). In the Alaska Coastal Current, stratification is enhanced by seasonal cycles in freshwater discharge and solar heating that result in a synchronous surface salinity minimum and surface temperature maximum in August (Royer 2005). Moreover, years of warmer SST are characterized by increased freshwater input and stronger water column stability in the Alaska Coastal Current (Brickley and Thomas 2004). In the California Current, cooler SST signals reduced stratification and increased availability of nutrients, stimulating primary production (Chavez and Messié 2009). Opposite SST-production relationships in the Alaska Coastal Current and California Current have been repeatedly observed in other studies: salmon survival rates, salmon growth, and rockfish growth all improve during warm conditions in the Alaska Coastal Current and cool conditions in the California Current (Mueter et al. 2002a, Wells et al. 2008, Black et al. 2008).

A quadratic model did not improve growth predictions compared to a model with separate SST effects for each current system, suggesting that temperature effects do not primarily arise from a direct relationship to fish metabolism across the range of observed temperatures in this study. Minimal juvenile dispersal (Miller and Shanks 2004) could allow black rockfish physiology to be locally adapted to environmental conditions– cool conditions during upwelling in the California Current and warm conditions during stratification in the Alaska Coastal Current.

Experimental studies with juvenile black rockfish suggest that optimal temperatures for growth are closer to 18° C (Boehlert and Yoklavich 1983), well beyond the range of SST observed in this study. If the optimal growth temperatures for subadult and adult black rockfish considered here are similar, the positive growth-SST relationship in the Alaska Coastal Current, but not the negative growth-SST relationship in the California Current, could be explained by a direct temperature relationship.

Kelp greenling growth was consistently faster in warmer California Current waters (summer average 11 to 15° C) as compared to cooler Alaska Coastal Current waters (summer average 8 to 13° C), suggesting that warmer temperatures result in increased growth rates of kelp greenling through direct effects on fish metabolism or increases in the quality of their benthic invertebrate prey. A direct temperature effect was not supported based on model selection results that favored current-specific SST effects over the quadratic growth response to SST anticipated when growth patterns are caused by an optimal growth temperature. A direct temperature effect is neither supported nor refuted by existing literature as optimal temperatures for growth in kelp greenling have not been studied. We cannot rule out the possibility that the positive growth-SST relationship observed here is the result of a direct temperature effect across suboptimal temperatures. Beyond this direct effect, temperature may have an indirect influence through lower trophic levels. Studies have demonstrated that warmer temperatures promote increased benthic invertebrate production at small spatial scales (10s and 100s of km). In both the Channel Islands and off Point Conception, California, warmer areas have higher invertebrate densities, faster invertebrate growth rates, and individuals allocate more energy to reproductive tissues despite lower availability and quality of food for filter-feeding invertebrates as compared to cooler areas (Phillips 2005, 2007, Blanchette et al. 2006). If the positive relationship between

benthic invertebrate production and SST occurs at large spatial scales, benthic invertebrates could be consistently more productive in the warmer California Current, supporting faster growth of their benthic fish predators. We are unaware of other studies that have compared benthic production between the Alaska Coastal Current and California Current that would provide further support for this mechanism.

The SST-growth patterns observed across current systems and species are consistent with pelagic nearshore food webs limited by a combination of nutrients and light at the level of primary producers, and benthic nearshore food webs limited by temperature effects on their benthic invertebrate prey. Bottom-up limitation in pelagic and benthic food webs could stem from different trophic pathways. During spring bloom conditions in pelagic systems, energy moves quickly and efficiently from large phytoplankton (e.g., diatoms) to large zooplankton (e.g., copepods) to fish. Energy pathways in benthic systems may operate more slowly, involving senescence of plankton blooms, formation of detritus, and passage through slow-growing benthic invertebrates (Rooney et al. 2006). Whether benthic invertebrate production is limited more by temperature or primary production (food) is a topic of vigorous debate (Menge and Menge 2013), but the combination of previous studies indicating temperature limitations on benthic invertebrates (Phillips 2005, 2007, Blanchette et al. 2006) and our results are consistent with temperature limitation.

2.4.2 Upwelling and chlorophyll

Despite consistent support for SST-growth relationships and expectations that all three environmental variables would form a suite of conditions associated with production, black rockfish growth was related to chlorophyll, but not to upwelling, and kelp greenling growth was related to upwelling, but not to chlorophyll. Other studies have found that environmental

variables do not consistently form a suite of conditions related to production (Mueter et al. 2002a, 2002b, Caselle et al. 2010). Thus, we interpret the apparent relationships and then consider the possible reasons for discrepancies among the SST, upwelling, and chlorophyll relationships, including alternative hypotheses and improper data resolution for the proposed hypotheses.

Incorporation of upwelling indices improved models of kelp greenling growth in the Alaska Coastal Current, suggesting that persistence of downwelling into the spring and summer months reduces kelp greenling growth in agreement with our hypothesis. Relaxation of downwelling during spring in the Alaska Coastal Current system allows deep nutrient-rich waters to move onto the shelf at depth and is associated with the start of the spring bloom by enhancing water column stability at the surface (Childers et al. 2005, Henson 2007). Increased availability of macronutrients to nearshore surface waters and increased water column stability are likely to enhance primary production by reducing nitrate (Stabeno et al. 2004) and light limitations (Henson 2007). The relationship between relaxed downwelling and production is consistent with growth rates of benthic mussels in a downwelling domain (Menge and Menge 2013).

The positive relationship between chlorophyll and rockfish growth suggests that bottom-up processes limit pelagic-feeding nearshore fish growth rates and provide a potential mechanism underlying positive relationships between fisheries catch data and chlorophyll concentrations (Ware and Thomson 2005, Chassot et al. 2007, Friedland et al. 2012). In places or years of higher chlorophyll concentrations, black rockfish may consume higher quality prey due to within-year increases in the size or energy of an individual prey item, such as a forage fish (Robards et al. 2002, Takahashi et al. 2012). To our knowledge, ours is the only study to

demonstrate a link between chlorophyll concentration and fish growth rates in the northeast Pacific Ocean. This may have resulted from our choice to examine chlorophyll data at localized spatial scales (1000s of km^2) and across sites with a wide range of chlorophyll concentrations. Sites near Vancouver Island had the highest chlorophyll concentrations of all study sites and variation across sites was much greater than the variability at any single site. Therefore, study designs making comparisons across sites may be more likely to detect a relationship between chlorophyll and fish growth.

A poor relationship between upwelling and black rockfish growth would typically suggest a lack of dependence on deep-water nutrient sources for production. Poor growth-upwelling relationships could arise from nearshore fronts preventing cool, nutrient rich upwelled waters from reaching nearshore habitats (Shanks et al. 2003, Shanks and McCulloch 2003) or strong upwelling drawing nutrients and phytoplankton away from nearshore regions (Cury and Roy 1989, Ware and Thomson 2005, Foley 2009). However, the negative growth-SST and positive growth-chlorophyll relationships in the California Current suggested cooler, presumably upwelled waters, stimulated primary production, and increased fish growth by increasing the availability of higher quality prey. The lack of a growth-upwelling relationship in light of other findings is more likely related to the coarse spatial resolution of the upwelling indices. Coastal upwelling indices used here are affected by large-scale atmospheric pressure systems >1000 km wide and ignore or at least minimize local influences (e.g., bathymetry and coastline shape) on mass transport that can prevail at smaller scales (Ladd et al. 2005, Broitman and Kinlan 2006). At small scales in nearshore waters, the coherence between upwelling and SST can be reduced if SSTs are modified by influences other than upwelling, such as freshwater discharge, solar heating, or tidal mixing (Huyer 1983).

The hypothesis relating kelp greenling growth to chlorophyll was not supported, suggesting that benthic invertebrate prey quality was not limited by primary production from phytoplankton throughout the summer. Chlorophyll concentrations are not always predictors of benthic mussel and barnacle growth (Phillips 2005, 2007; Blanchette et al. 2006) and support the possibility of alternative hypotheses. Terrestrial and macroalgae sources of carbon may supplement or displace phytoplankton production (Foley 2009, Tallis 2009) and drive interannual differences in nearshore fish growth (Schoch and Chenelot 2004, Miller et al. 2011). The positive growth-SST relationships may suggest temperature-limited feeding and digestion rates of benthic invertebrates across our study range so that even a relatively low level of primary production is able to satiate invertebrates (Phillips 2005, Blanchette et al. 2007). Finally, the community dynamics of benthic invertebrates are complex, with conditions that promote growth (i.e., prey quality) occurring on shorter timescales (within a year) and differing from conditions that promote recruitment (i.e., prey quantity) on longer timescales (> 1 year). Thus, while we acknowledge that there may be lagged environmental effects on prey quantity owing to trophic interactions within these nearshore pelagic and benthic food webs, it was beyond the scope of our study to attempt to model the diversity of such lags characterizing the variety of life histories and trophic levels represented by species in the diets of kelp greenling and black rockfish. Our hypotheses focused on changing conditions controlling first-order effects on prey quality, rather than the prey abundances, which are affected by recruitment processes and complex trophic interactions.

In addition, both upwelling events and their associated chlorophyll blooms operate on shorter timescales (days) than the six month averages considered in this study. Short-term variability in wind stress with periods of several days can cause upwelling, even during a month

when the mean wind stress is not upwelling favorable (Huyer 1983). Timing of upwelling and chlorophyll blooms can be critical to seasonally occurring processes such as reproduction, recruitment processes, and juvenile and adult growth (Barth et al. 2007, Sydeman and Bograd 2009, Brander 2010, Black et al. 2011, Takahashi et al. 2012). Still, it can be difficult to identify environmental variables that adequately capture the specific timing or duration of critical processes that matter most to reproduction, growth, or survival. Several possible methods have been suggested with varying success (Lynn et al. 2003, Holt and Mantua 2009, Menge and Menge 2013).

2.4.3 Research and management implications

Indices of production from otolith growth proxies have been found to be useful for studies of other marine fish and invertebrate populations (Black et al. 2009, 2010, 2011). Stock assessment models used for fisheries management may benefit from indices of nearshore production as many commercial fish species have critical early life history stages in nearshore systems (Agardy et al. 2005, Laurel et al. 2007, Echave et al. 2012, Johnson et al. 2012). Spatial differences in nearshore nursery habitat availability has been tied to adult stock size (Fodrie and Levin 2008, Sundblad et al. 2013) and increases in the Gulf of Alaska commercial catch during the 1980s and 1990s were concurrent with sustained increases in nearshore production linked to basin-scale oceanographic processes (Robards et al. 1999, Mueter and Norcross 2000). Indices of production are also useful toward advancing an ecosystem-based approach to management. For instance, ecosystem-based fisheries management can be implemented incrementally by incorporating ocean productivity indices into single-species stock assessment models, such as through dynamic models of fish growth from which harvestable biomass is calculated, or more

holistically, by considering implications of whole ecosystem productivity on total fishery yields (O'Boyle et al. 2012).

2.4.4 Conclusions

We uncovered bottom-up relationships in nearshore pelagic food webs that are consistent with mechanisms identified from offshore (continental shelf) pelagic food webs, including the influence of water column stability (indicated by SST) and primary production (indicated by cholorophyll) on fish growth. In benthic nearshore food webs, our results are consistent with temperature limitation acting directly on fish or indirectly through their prey (i.e., benthic invertebrates). Warming conditions and shoaling thermoclines are expected to reduce production in low latitude pelagic systems that are already nutrient limited (Behrenfeld et al. 2006) and to increase production in higher latitude pelagic systems (Mueter et al. 2009). Our results extend these forecasts to nearshore pelagic systems, and add the prediction that warming will also increase nearshore benthic production in the near term for the California Current and Alaska Coastal Current systems.

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Table 2.1. Collection sites, code, dates and sample sizes for black rockfish and kelp greenling otoliths. The buffered site area includes a 100 km buffer around the site used to calculate mean sea surface temperature.

Site	Site Code	Black Rockfish	Kelp Greenling	Collection Dates	Site Area (km^2)	Buffered Site Area (km^2)
Paul Island, Alaska Peninsula, southwest Alaska	APEN	35	0	July 2009	4,137	53,554
Katmai National Park and Preserve, Alaska Peninsula, southcentral Alaska	KATM	39	50	July 2010	1,698	20,823
Western Prince William Sound, southcentral Alaska	WPWS	40	84	June and August 2010	1,910	32,187
Elfin Cove, northern Chichagof Island, Southeast Alaska	ELFI	45	43	May 2011	1,171	18,758
Whale Bay, southern Baranof Island, Southeast Alaska	WHAL	44	41	May and June 2011	1,516	24,313
Nuchatlitz, west Vancouver Island	NUCH	45	61	May, June and September 2010	1,062	16,959
Clayoquot Sound, west Vancouver Island	CLAY	47	43	May 2010 and July 2011	3,344	23,622
Neah Bay, Olympic Peninsula, Washington	WASH	50	50	Throughout 2010 and 2011	3,650	28,976
Big Sur, central California	BIGS	28	18	September 2010	2,616	14,528

Table 2.2. Interseries correlations (measure of common signal strength in each time series) for growth increments of black rockfish and kelp greenling captured at sites in the northeast Pacific Ocean. Sample size (n) refers to the number of fish that were ≥5 yr old and could be cross-dated.

Site	Black Rockfish	Kelp Greenling
APEN	0.54 (n=26)	n/a
KATM	0.41 (n=35)	0.67 (n=6)
WPWS	0.37 (n=36)	0.70 (n=9)
ELFI	0.41 (n=35)	0.47 (n=23)
WHAL	0.41 (n=26)	0.45 (n=28)
NUCH	0.41 (n=28)	0.51 (n=23)
CLAY	0.49 (n=37)	0.57 (n=14)
WASH	0.49 (n=29)	0.51 (n=31)
BIGS	0.58 (n=11)	0.50 (n=9)

Table 2.3. Model selection results for predicting black rockfish and kelp greenling growth using sea surface temperature (SST; Apr-Sep), upwelling (UW; Apr-Sep), and chlorophyll concentrations (Chla; Apr-Sep). Models in bold provided the best fit for each model group as judged by AIC values. The degrees of freedom (df) and sample size (n), or unique number of growth increments, are also reported for each model.

Species	Model Group	Model	df	n	ΔAIC
Black Rockfish	SST	**age + current * SST**	**13**	**2991**	**0**
		age + SST + SST^2	12	2991	11.7
		age + current	11	2991	14.3
		age	10	2991	15.0
		age + SST	11	2991	15.6
	UW	**age + current**	**11**	**3129**	**0**
		age	**10**	**3129**	**0.5**
		age + current * UW	13	3129	1.0
		age + UW	11	3129	2.5
	Chla	**age + current * Chla**	**13**	**1826**	**0**
		age + Chla	**11**	**1826**	**3.0**
		age + current	11	1826	8.6
		age	10	1826	9.4
Kelp Greenling	SST	**age + current * SST**	**9**	**987**	**0**
		age + SST	**7**	**987**	**1.4**
		age + SST + SST^2	8	987	2.4
		age + current	7	987	10.3
		age	6	987	24.6
	UW	**age + current * UW**	**9**	**1102**	**0**
		age + current	7	1102	9.2
		age + UW	7	1102	20.7
		age	6	1102	23.2
	Chla	**age + current**	**7**	**949**	**0**
		age + current * Chla	9	949	2.3
		age	6	949	14.2
		age + Chla	7	949	15.4

Table 2.4. Correlation strength among sea surface temperature (SST; Apr-Sep; 1982-2009), upwelling (UW; Apr-Sep; 1982-2011), and chlorophyll-*a* concentrations (Chla; Apr-Sep;2003-2011) at each site in the Alaska Coastal Current (ACC) and California Current (CC) as indicated by the coefficient of determination (r^2) from linear regression. Negative values denote inverse correlations.

Site	SST vs Chla	SST vs UW	UW vs Chla
APEN	0.33	-0.02	-0.01
KATM	0.27	-0.01	0.13
WPWS	-0.51	0.00	-0.25
ELFI	0.04	0.05	0.28
WHAL	0.02	0.05	0.02
ACC average	0.03	0.01	0.03
NUCH	-0.01	-0.07	0.10
CLAY	0.00	-0.09	0.24
WASH	0.07	-0.19	0.20
BIGS	0.18	-0.12	-0.15
CC average	0.06	-0.12	0.10

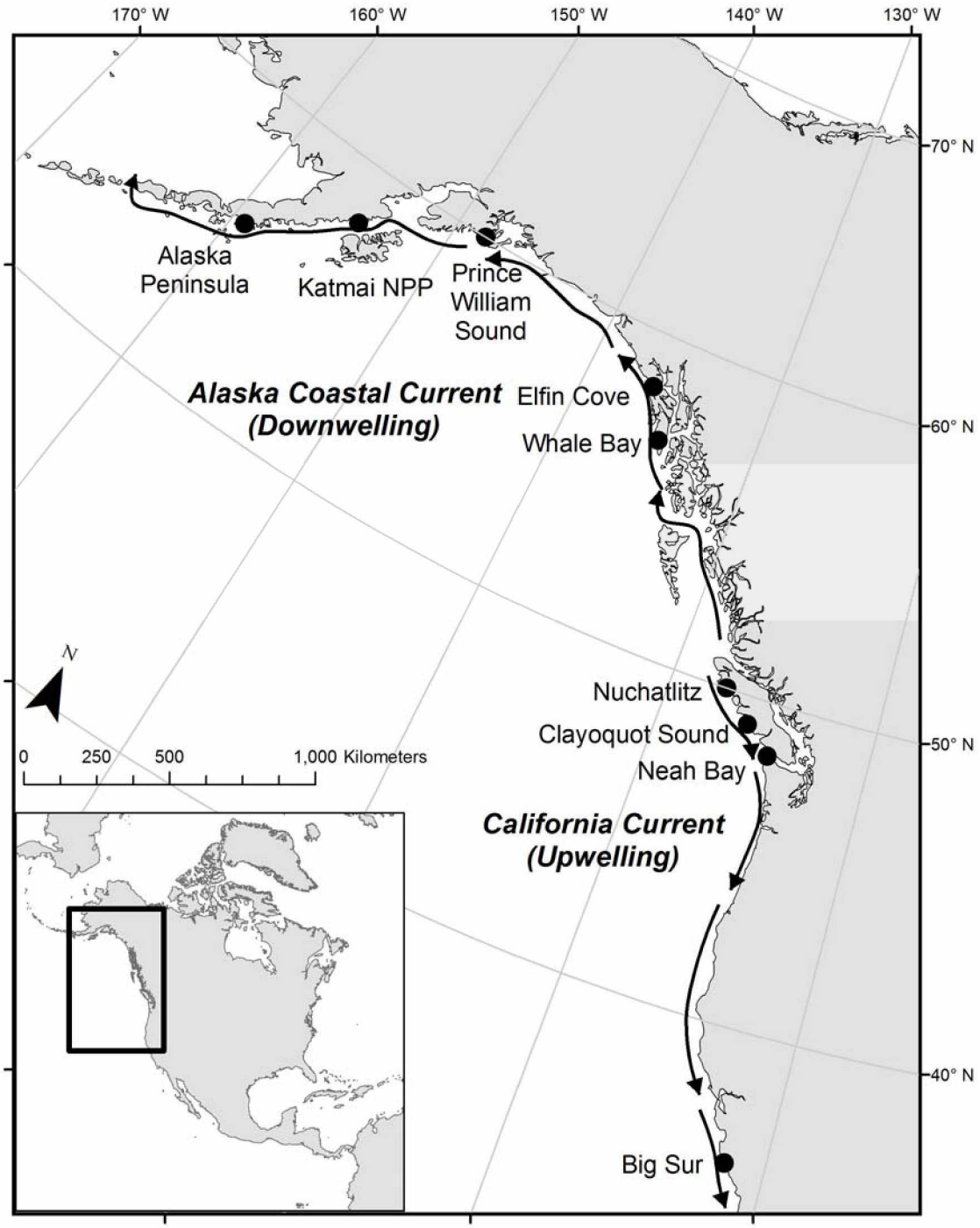

Figure 2.1. Nearshore fish collection sites (solid dots) and generalized nearshore current flow in summer (arrows) in the Alaska Coastal Current and California Current.

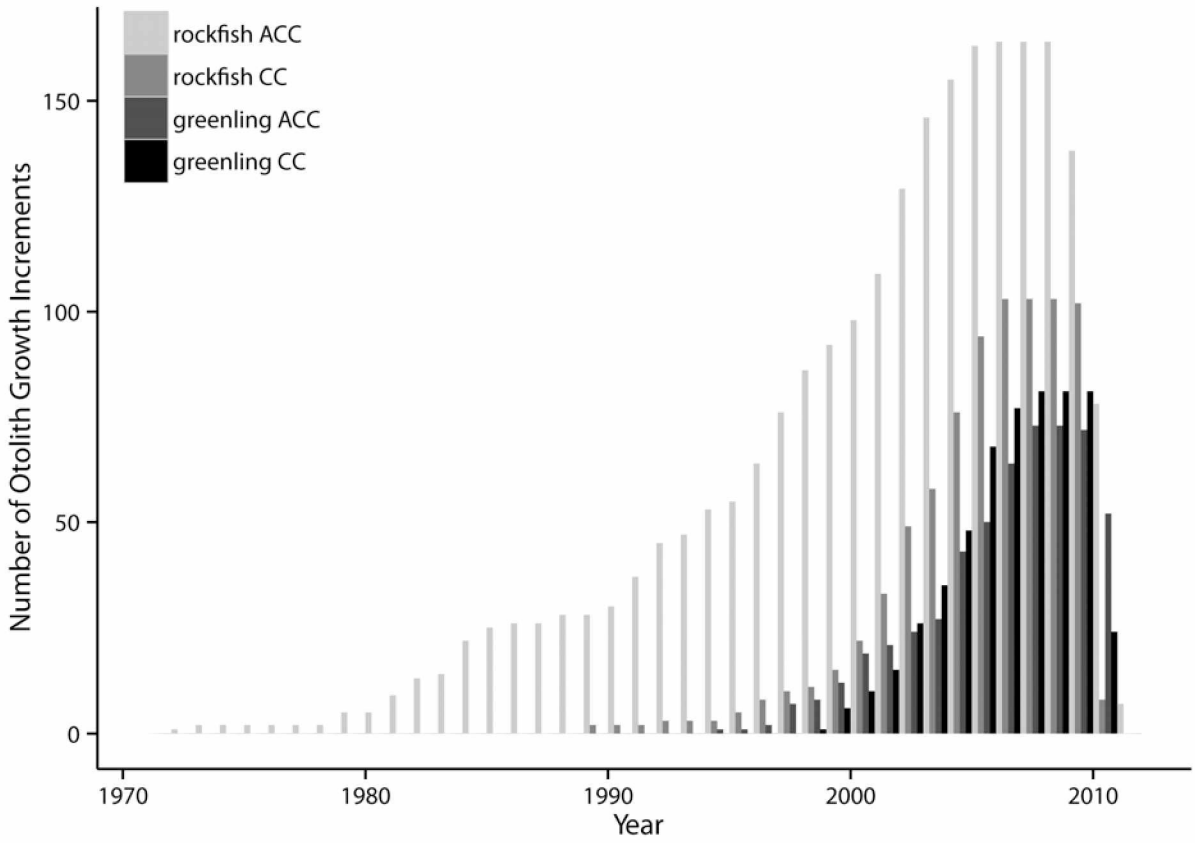

Figure 2.2. Annual otolith growth increment sample sizes by growth year for black rockfish and kelp greenling captured in the Alaska Coastal Current (ACC) and California Current (CC). All growth increments were from individuals at least 5 yrs old and and the increments measured spanned the sub-adult and adult growth history (increments representing age-1 growth and beyond). Black rockfish are longer lived than kelp greenling and provided longer data records, particularly in the ACC. Sea surface temperature analyses included increments during 1982-2009, upwelling analyses included all increments, and chlorophyll analyses included increments during 2003-2011.

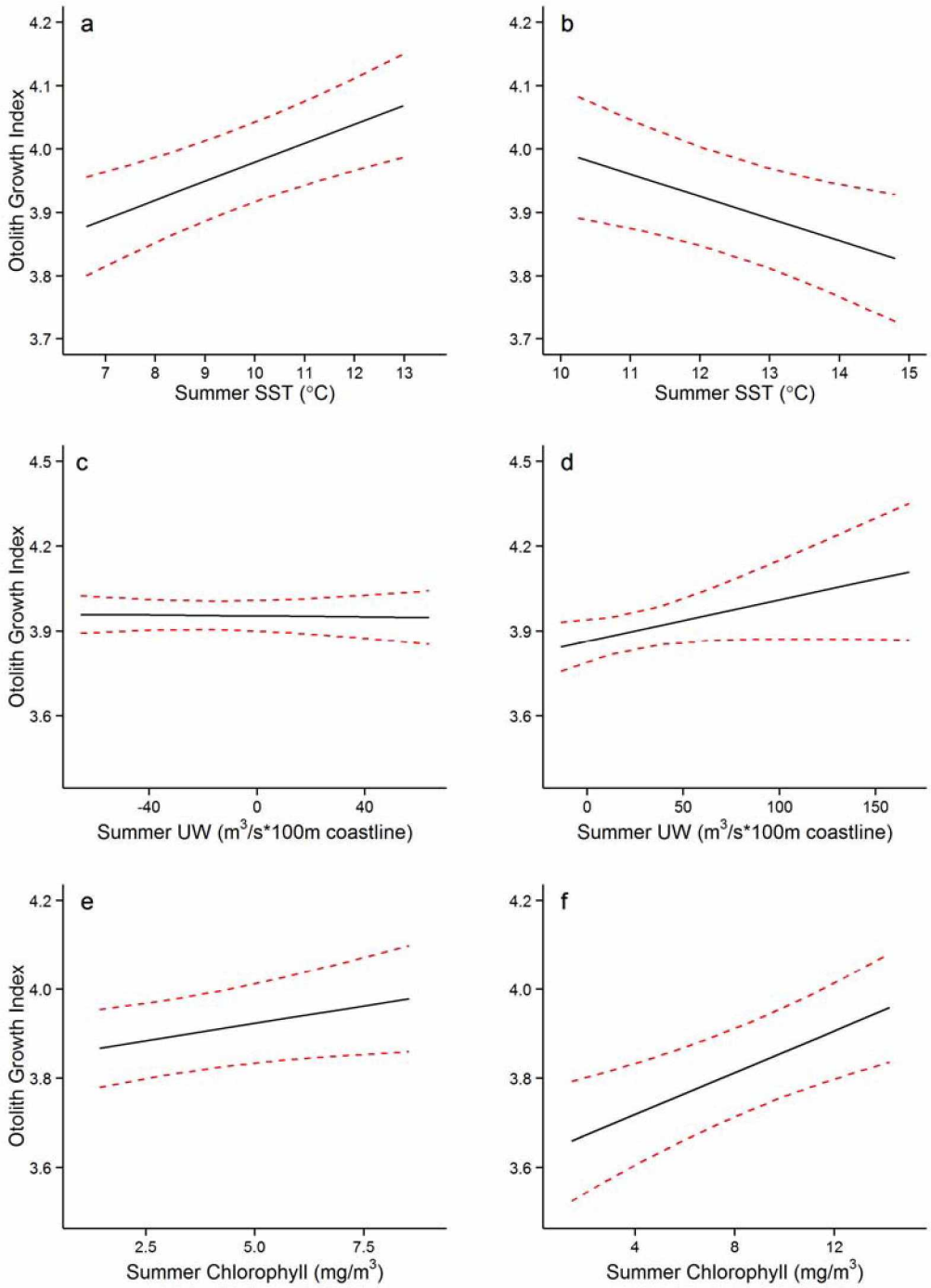

Figure 2.3. Mean growth response of nearshore pelagic-feeding black rockfish to sea surface temperature (SST; monthly average Apr-Sep; a & b), upwelling (UW; monthly average Apr-Sep; c & d), and chlorophyll-a (monthly average Apr-Sep; e & f) in the Alaska Coastal Current (left column) and California Current (right column). Dashed lines denote 95% confidence intervals. Model selection criteria suggest that inclusion of SST and chlorophyll improve predictions of annual rockfish growth, while including the upwelling index did not improve the fit.

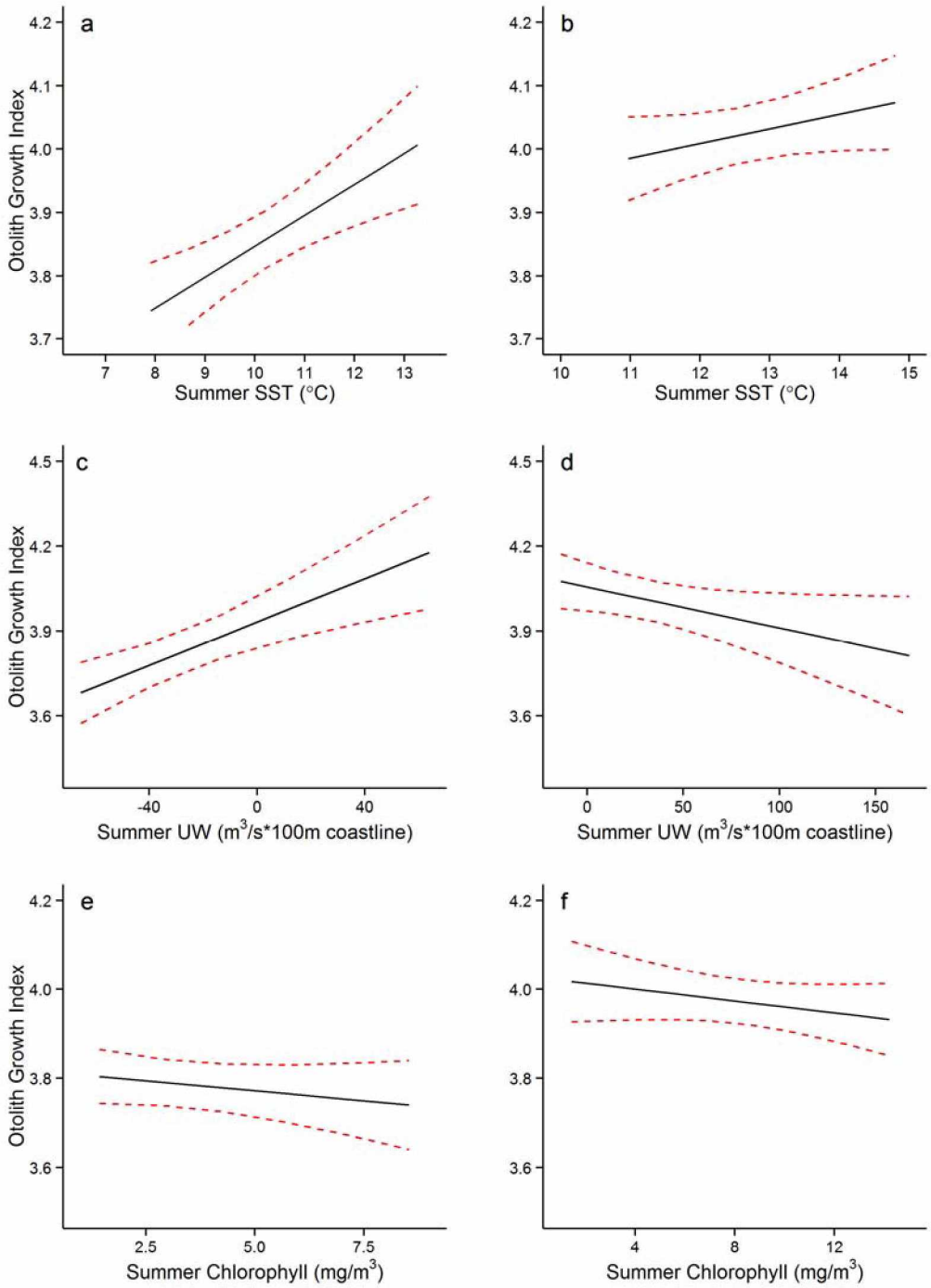

Figure 2.4. Mean growth response of nearshore benthic-feeding kelp greenling to sea surface temperature (SST; monthly average Apr-Sep; a& b), upwelling (UW; monthly average Apr-Sep; c& d), and chlorophyll-a (monthly average Apr-Sep; e & f) in the Alaska Coastal Current (left column) and California Current (right column). Dashed lines denote 95% confidence intervals. Model selection criteria suggest that SST and upwelling effects improved predictions of annual greenling growth, while including chlorophyll did not improve the fit.

2.7 Appendices

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Best regards,
David Douglas

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Appendix 2.1. Permission to use manuscript in dissertation from David Douglas

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Thomas Helser - NOAA Federal <thomas.helser@noaa.gov> Thu, Jan 8, 2015 at 2:46 PM
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Appendix 2.2. Permission to use manuscript in dissertation from Thomas Helser

Chapter 3: Influence of basin and local-scale conditions on nearshore production in the northeast Pacific Ocean[1]

Abstract

Nearshore systems are among the most productive yet vulnerable marine habitats owing to their juxtaposition at the marine-terrestrial interface. To understand how basin and local-scale processes may influence nearshore habitat-dependent species, we developed an annual index of nearshore production from the otolith growth increments of pelagic- and benthic-feeding nearshore resident fishes at nine sites in the California and Alaska Coastal currents spanning 1972-2010. We explored the influence of basin- and local-scale indicators across all seasons and with lags up to two years to account for changes in the quantity (1-2 year time lags) and quality (within-year relationships) of prey. Relationships linking fish growth to basin-scale (Pacific Decadal Oscillation, North Pacific Gyre Oscillation, and Multivariate El Niño Southern Oscillation Index) and local-scale (sea surface temperature, sea surface height anomalies, upwelling, and photosynthetically active radiation) environmental conditions varied by species and current system. Growth of pelagic-feeding Black Rockfish increased with cool basin-scale conditions in the California Current and warm local-scale conditions in the Alaska Coastal Current, consistent with existing hypotheses linking climate to pelagic production on continental shelves in the region. Benthic-feeding Kelp Greenling grew faster both during and subsequent to warm conditions in the Alaska Coastal Current as indicated by both basin- and local-scale conditions. In the California Current, Kelp Greenling relationships were more complex, with faster growth related to within-year warm conditions and cool conditions during lagged

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[1] von Biela, V.R. et al. In prep. Influence of basin and local-scale conditions on nearshore production in the northeast Pacific Ocean. Marine and Coastal Fisheries.

relationships. These opposite relationships may reflect differences in conditions that promote quantity versus quality of their benthic invertebrate prey in the California Current, thus motivating new hypotheses linking environmental conditions to nearshore production in benthic food webs.

3.1 Introduction

Understanding fluctuations in marine fish and ecosystem production is a pressing research goal as scientists and policy makers address climate change forecasts (Hollowed et al. 2011, Link et al. 2012). Commercial fishing records and stock assessment surveys provide a wealth of observational data needed to understand climatic drivers of fish production in continental shelf systems (Hare and Mantua 2000, Hollowed et al. 2001, Noakes and Beamish 2009, Mueter et al. 2009, Litzow and Mueter 2014), but not all marine ecosystems are commercially fished. Nearshore systems are economically important for recreational fishing, diving, and wildlife viewing, but seldom targets of commercial fisheries that provide catch, stock assessment, and recruitment data needed to estimate production or understand climatic drivers (Cooke and Cowx 2004, 2006, Agardy et al. 2005). Nearshore systems are among the most productive areas of the ocean, function as critical spawning and rearing habitat for commercial and non-commercial species, and support high biodiversity (Kruse and Tyler 1989, Dean et al. 2000, Agardy et al. 2005, Laurel et al. 2007, Doyle et al. 2009). A lack of available data in nearshore systems is compounded by complex interactions of atmospheric, oceanographic, watershed, and human influences at the marine-terrestrial interface (Cloern and Jassby 2008). To provide insights about nearshore biological responses to basin and local-scale processes, we developed an annual index of nearshore production from growth rates of pelagic- and benthic-feeding nearshore resident fishes at nine sites in the California and Alaska Coastal currents.

Relationships between basin-scale climate indices and nearshore fish growth would imply strong linkage between local biology and global climate dynamics. Basin-scale climate indices

could influence nearshore systems through their linkages to offshore or terrestrial systems, as climate indices correlate well with offshore indicators, such as sea surface temperature (SST), salinity, and upwelling (Di Lorenzo et al. 2008, Ainley and Hyrenbach 2010), and with terrestrial indicators, such as freshwater discharge (Royer et al. 2001, Papineau 2001, Neal et al. 2002, Hickey et al. 2010). Interpretation of basin-scale relationships and proposed linkages to nearshore responses could be improved by an investigation of organismal growth response to local conditions. The Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and El Niño Southern Oscillation (ENSO), represent both decadal (e.g. PDO and NPGO) and interannual (e.g. ENSO) scales of climate variability in the northeast Pacific (Hollowed et al. 2001) and are among the most consistent predictors of marine and terrestrial ecosystem production in the North Pacific Ocean and western United States, respectively (Neal et al. 2002, Mundy 2005, Spies 2007, Menge et al. 2009, Black 2009, Sydeman et al. 2013, Di Lorenzo et al. 2013).

Analyses spanning multiple seasons at plausible biological time lags allow for consideration of interannual shifts in phenology and prey abundance in climate-growth relationships. For instance, the seasonal timing of upwelling in the California Current can alter primary production, recruitment of benthic invertebrates, zooplankton abundance, rockfish growth, and seabird reproduction, even when normal upwelling conditions prevailed later in the summer (Barth et al. 2007, Shanks and Roegner 2007, Black et al. 2011). Time lags are also necessary when linking predator production with environmental conditions through trophic interactions (*sensu* Post 2004). For example, lags are necessary when predators are limited by the availability of prey that are $\geq$1 year old and prey abundance is determined by conditions in early life history (Miller and Sydeman 2004, Frederiksen et al. 2006, von Biela et al. 2011).

Black Rockfish *Sebastes melanops* and Kelp Greenling *Hexagrammos decagrammus* are common nearshore resident fishes with similar geographic distributions spanning the California and Alaska Coastal Currents in the northeast Pacific Ocean. Individuals of both species have small home ranges in rocky reef habitats with canopy kelp (*Macrocystis pyrifera* and *Nereocystis luetkeana*) (Freiwald 2009, Love 2011, Pirtle et al. 2012). Black Rockfish are pelagic-feeding generalists targeting forage fish, including Pacific Herring (*Clupea pallasi*), Pacific Sand Lance (*Ammodytes hexapterus*), and juvenile salmon (*Oncorhynchus* spp.), as well as invertebrates, such as crab megalopae (Rosenthal 1983, Love et al. 2002, Love 2011, Sturdevant et al. 2012). Kelp Greenling are benthic-feeding generalists, foraging on a variety of benthic invertebrates including amphipods, snails, sea cucumbers, decorator crabs, and brittle stars (Moulton 1977, Hines 1982, Rosenthal 1983, Love 2011). The age-structure of prey consumed by benthic-feeding Kelp Greenling is poorly documented, but the size range of crabs consumed by other benthic predators suggests that prey are often age 0 or age 1 (Yang 1993).

In this study, we explored the influence of basin- and local-scale environmental indices across seasons and years on growth of two nearshore fishes, Black Rockfish and Kelp Greenling, in the California and Alaska Coastal Currents. *A priori*, we posited that fish growth is related to both basin- and local-scale indices (Figure 3.1) and categorized relationships in terms of 'warm', water column stabilizing or 'cool', destabilizing effects. More specifically, we hypothesized that nearshore pelagic rockfish will benefit from cooler conditions in the California Current and warmer conditions the Alaska Coastal Current (Polovina et al. 1995, Gargett 1997, von Biela et al. 2015), while nearshore benthic greenling will benefit from warmer conditions in both current systems (Phillips 2005, Blanchette et al. 2006, von Biela et al. 2015). In our analysis, we considered the time lags when basin- and local-scale indices are related to nearshore fish growth and production. Lagged relationships were intended to reflect changes in prey quantity through

trophic interactions, while current year relationships were taken to indicate changes in prey quality associated with feeding conditions as well as the quantity of age-0 prey. Lags of up to two years were considered to match the age classes of probable forage fish and invertebrate prey (Hatch and Sanger 1991, Yang 1993, Van Pelt et al. 1997).

3.2 Methods

Nearshore production was indexed using annual growth increments recorded in Black Rockfish and Kelp Greenling otoliths collected at nine sites in the California Current and Alaska Coastal Current (Figure 3.2). Study sites were characterized by rocky reef habitat, and the presence of macrophytes (kelp) and sea otters *(Enhydra lutris)*, a keystone predator in nearshore systems known to increase community diversity and kelp production via top-down control of major kelp grazers, such as sea urchins (*Strongylocentrotus spp.*; Steneck et al. 2002). Details of collections, otolith sectioning, otolith measuring, and crossdating procedures were previously described (Chapter 2). Briefly, fish were collected using a combination of hook and line sampling, trammel netting, and spear fishing from shallow (< 15 m) rocky reef habitats from 2009 to 2011. Otoliths were removed, sectioned, and mounted on slides to measure annual increment widths on digital images captured with a digital camera (Leica DFC 425 or 450) mounted on a stereomicroscope (Leica MZ6 or M60) under 20x to 40x magnification following Black et al. (2005). Dendrochronology crossdating procedures were used to verify growth synchrony across individuals before further analysis (Black et al. 2005). To establish a series of growth increments from an individual for cross-dating, only fish 5 yr and older at capture were included in this study (age range 5 to 40 yr old) and the increments measured spanned the sub-adult and adult growth history (increments representing age-1 growth and beyond). Annual growth increments spanned 1972-2010 for Black Rockfish and 1994-2010 for Kelp Greenling, however the years 2000-2010 are best represented because younger fish also provided data from these years.

Growth was compared to basin-scale climate indicators and local indicators across seasons with time lags up to two years. Seasons were defined as: autumn (Oct-Dec), winter (Jan-Mar), spring (Apr-Jun), and summer (Jul-Sep) following (Cummins and Masson 2014). The PDO, NPGO, and the Multivariate ENSO index (MEI) were selected as basin-scale climate indicators. The PDO is the leading principal component of monthly SST and NPGO is the second dominant mode of sea surface height anomalies (SSHa) in the North Pacific Ocean (Mantua et al. 1997, Di Lorenzo et al. 2008). Positive values of PDO indicate warm coastal SST throughout the northeast Pacific Ocean, weaker upwelling and decreased precipitation in the California Current, and stronger downwelling and increased precipitation in the Alaska Coastal Current (Mantua et al. 1997, Royer 2005). Positive values of NPGO indicate enhanced transport of the North Pacific Current as well as increased transport of both the Alaska Coastal and California Currents (Di Lorenzo et al. 2008). Increased transport in the California Current is associated with stronger upwelling, higher sea surface salinity and nutrient concentrations, weaker thermoclines, decreased water column stability and cool conditions in the California Current (Di Lorenzo et al. 2008, 2009). Increased transport of the Alaska Coastal Current is associated with warmer conditions in the Gulf of Alaska as the Subarctic Gyre intensifies, and drawing more warm waters from the south (Di Lorenzo et al. 2008, Danielson et al. 2011). The MEI is the leading principal component of six variables over the tropical Pacific: sea level pressure, meridional and zonal wind components, cloudiness, surface air temperature, and SST (Wolter and Timlin 1998). Positive values of MEI are associated with ENSO conditions, including a warmer, fresher and more stable water column with low nutrient concentrations in the eastern Pacific Ocean (Wolter and Timlin 1998). The three basin-scale indices interact with ENSOs centered over the eastern Pacific modifying the Aleutian Low Pressure system and PDO, while ENSOs centered over the central Pacific modify the North Pacific Oscillation and NPGO (Di Lorenzo et al. 2013). Monthly values

for PDO, NPGO, and MEI were obtained from the Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/pdo/), the Department of Ocean Climate & Ecosystem Science at Georgia Tech (http://www.o3d.org/npgo/), and the NOAA Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/enso/mei/), respectively.

Local-scale climate indices included SST, SSHa, photosynthetically active radiation (PAR), and upwelling. Environmental variables were selected because they are either used to derive (SST and SSHa) or track the basin-scale climate indicators and are useful for predicting biological responses (Mantua et al. 1997, Royer et al. 2001, Papineau 2001, Neal et al. 2002, Di Lorenzo et al. 2008, Hickey et al. 2010, Ainley and Hyrenbach 2010). Sea surface temperature measures the heat near the surface of the ocean. Winds, currents, and the heat content of the water column all influence SSHa, with lower values indicating offshore water movement during periods of upwelling and reduced heat content as heat causes water column expansion (Wolf et al. 2009). Photosynthetically active radiation is a measure of the energy available for photosynthesis at the surface of the ocean in the waveband used by primary producers (400 - 700 nm). Coastal upwelling indices are derived from wind stress, with positive values indicating upwelling and negative values indicating downwelling. In the California Current, upwelling values are generally positive so that increasing values are associated with more upwelling and cooler, less stable conditions. In the Alaska Coastal Current, the upwelling values are typically negative so that increasing values are associated with the relaxation of downwelling (values near zero) and a lack of vertical mixing that promotes stability and 'warm' conditions. Warmer, more stable, conditions were assumed to be associated with higher SST, SSHa, and PAR in both current systems, increased upwelling (i.e., relaxed downwelling) in the Alaska Coastal Current, and decreased upwelling (i.e., relaxed upwelling) in the California Current.

For gridded environmental data sets (SST, SSHa, and PAR), the study site area included a 100 km buffer to increase the number of grid cells sampled and site area (range 14,000 to 60,000 km^2). In all cases, the spatial extent of calculations was truncated at the 200 m isobath. Monthly SST averages were extracted from AVHRR PathFinder version 5.0 satellite SST data for each site from 1982 to the year prior to fish collection (http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/userguide.html). Monthly SSHa were obtained via satellite altimetry measurements from the AVISO product (http://coastwatch.pfeg.noaa.gov/erddap/griddap) for each site from 1993 to the year prior to fish collection. Monthly PAR averages were obtained from MODIS Terra satellites (http://oceandata.sci.gsfc.nasa.gov/MODIST/Mapped/Monthly/4km/par/) from 2000 to the year prior to fish collection. In the northern part of our study range, seasonally low light conditions prevented PAR detection by satellites and resulted in a data gap for Nov-Jan. Therefore, there are no models for autumn, and the winter season was taken to be the average of February and March values only. Monthly averaged upwelling indices were obtained from the Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/) for a representative latitude and longitude at each study area and for all years with increment growth data.

Models were formulated to allow the relationships between annual otolith increment width and each basin or local-scale indicators to vary by current system and recognize that growth increment width is related to the age of the fish during increment formation and that these relationships may vary across sites and across individual fish. All models included age during increment formation to account for faster growth when fish are young (Morrongiello et al. 2011). Annual otolith increment widths and age were log-transformed prior to analysis to achieve homoscedasticity and a linear relationship between these two variables. In addition to an overall growth intercept (increment width at age 0) across all sites, increment widths were allowed to

vary across individual fish by including random intercepts specific to each individual fish, nested within random site-specific intercepts. Black Rockfish models also included a random slope term in addition to the age effect that modifies the effect of age on growth for individual fish nested within sites, essentially fitting an individual growth trajectory to each fish. Models predicting Kelp Greenling annual growth increments did not converge when random slopes were included for each individual. Therefore only random intercepts were included, assuming that all individuals grow at the same rate after accounting for environmental influences on growth. Only one environmental index was considered at a time and indices were scaled (mean±SD = 0±1.0) prior to analysis so that model coefficients are comparable across analyses, with larger magnitude coefficients indicating stronger relationships.

The width of an annual increment in year t, at site k, for individual i is y_{tki} and is estimated as:

$$y_{tki} = (\alpha + a_k + a'_{i(k)}) + (\beta + b_k + b'_{i(k)})X_{ti} + \gamma_c EI_{tk_L} + \varepsilon_{tki}\,, \qquad (3.1)$$

where α is the fixed intercept, and a_k and $a'_{i(k)}$ are the random deviations in the intercept for each site, k, and individual, i, nested within sites, respectively. The age of individual i in year t (X_{ti}) is included to capture the decline in growth with age and is described by a fixed slope, β, a random site deviation, b_k, and an individual deviation $b'_{i(k)}$. The growth response to each environmental index (EI_{tk_L}) in year t, at site k, with lag L differs by current system as a fixed effect (γ_c). For basin-scale indicators, the environmental index is not site specific and becomes EI_{t_L} The variance-covariance structure of the random effects is given by:

$$\boldsymbol{b_k} = \begin{bmatrix} a_k \\ b_k \end{bmatrix} \sim N(0, \boldsymbol{\Psi_1}) \qquad \boldsymbol{b_{i(k)}} = \begin{bmatrix} a'_{i(k)} \\ b'_{i(k)} \end{bmatrix} \sim N(0, \boldsymbol{\Psi_2})$$

where $\boldsymbol{b_k}$ is the site level random effects vector, assumed to be independent for different k, $\boldsymbol{b_{i(k)}}$ is the individual within site-level random effects vector, assumed to be independent for different i, k

and independent of $\boldsymbol{b_k}$, and $\boldsymbol{\Psi_1}$ and $\boldsymbol{\Psi_2}$ are unstructured 2x2 variance-covariance matrices. If a model did not converge with this random effects structure, a simplifying assumption was imposed whereby the individual-level random intercepts and slopes are assumed to be independent in a diagonal 2x2 variance-covariance matrix. Independence of the random slopes and intercepts is unlikely, but this assumption is less restrictive than eliminating the random slopes when these models fail to converge. The errors ε_{tki} are assumed to be first-order autocorrelated within individuals and independent of the random effects, such that:

$$\varepsilon_{tki} = \phi \cdot \varepsilon_{t-1,ki} + \nu_t \qquad \nu_t \sim N(0, \sigma_\nu^2),$$

where ϕ is the first-order autoregressive coefficient and ν_t is a normally distributed variable with mean 0 and variance σ_ν^2.

The Kelp Greenling model without random slope effects was:

$$y_{tki} = \left(\alpha + a_k + a'_{i(k)}\right) + \beta X_{ti} + \gamma_c EI_{tk_L} + \varepsilon_{tki}. \qquad (3.2)$$

Models were initially fitted using maximum likelihood for model comparisons, with the best model refitted using restricted maximum likelihood to obtain unbiased coefficients (Pinheiro and Bates 2000). Nested model formulations with and without each environmental effect were compared using the Akaike Information Criterion to determine the best fit (Burnham and Anderson 2002). Basin and local-scale effects were considered significant if the AIC value decreased by 2.0 or more as compared to the same model without the basin or local-scale effect and the coefficient describing the effect was statistically significant ($P < 0.05$). All analyses were conducted in package 'nlme' (Pinheiro and Bates 2000) using R statistical software (R Development Core Team 2013). Otolith growth indices were not converted to changes in somatic size for any analysis as otolith growth indices likely reflect overall body condition and not just changes in length (Black et al. 2013).

3.3 Results

Black Rockfish and Kelp Greenling growth across the California Current and Alaska Coastal Current systems was related to PDO, NPGO and MEI based on improvements in model AIC values (Table 3.1). For Black Rockfish, models with PDO were favored in 6 of the 12 seasons examined, with 3 of the seasons occurring two years prior to growth ($winter_{L2}$-$summer_{L2}$; subscripts denote lag length in years) and the other 3 relationships occurring throughout the prior and current year ($winter_{L1}$, $winter_{L0}$, and $summer_{L0}$) (Table 3.2). Black Rockfish growth was related to NPGO with a lagged relationship encompassing 5 seasons starting two years prior through the previous autumn ($autumn_{L2}$-$autumn_{L1}$) and during the current year (3 consecutive seasons, autumn-spring)(Table 3.2). Black Rockfish growth was related to MEI with a 2 year lag ($winter_{L2}$-$spring_{L2}$) and during the year of growth over 5 consecutive seasons ($summer_{L1}$-summer).

Among Kelp Greenling growth models, inclusion of PDO improved models in 10 of the 12 seasons (Table 3.1) with most of the relationships occurring during a consecutive group of 7 seasons with a lag ($autumn_{L2}$-$spring_{L1}$) and 3 seasons without a time lag ($autumn_{L1}$ and spring-summer). Inclusion of NPGO improved models of Kelp Greenling growth only during the year of growth (all 4 seasons in the current year, autumn-summer). The MEI was related to Kelp Greenling growth in 5 seasons with lags (3 consecutive seasons, $autumn_{L2}$-$spring_{L2}$; 2 consecutive seasons, $autumn_{L1}$ -$winter_{L1}$) and 2 seasons without time lags (autumn and summer).

Current-specific coefficients indicated that cool conditions were generally associated with faster Black Rockfish growth in the California Current (17 of 18 significant coefficients, Table 3.2, Figure 3.3). Specifically, Black Rockfish growth was inversely related to PDO, with (3 consecutive seasons, $winter_{L2}$-$summer_{L2}$) and without lags (summer), positively related to NPGO with (4 consecutive seasons, $winter_{L2}$-$autumn_{L1}$) and without lags (3 consecutive seasons, autumn-

spring), and negatively related to MEI with (2 consecutive seasons, $winter_{L2}$-$spring_{L2}$) and without lags (4 consecutive seasons, $summer_{L1}$-spring). Black Rockfish growth in the Alaska Coastal Current had fewer significant relationships among the current-specific coefficients (9 coefficients, Table 3.2). Growth was both negatively ($spring_{L2}$) and positively ($winter_{L1}$ and winter) related to PDO, positively related to NPGO during 4 seasons ($autumn_{L2}$-$winter_{L2}$ and $summer_{L2}$-$autumn_{L1}$), negatively related to MEI in 1 season (winter), and positively related to MEI in 1 season (summer).

Current-specific coefficients from Kelp Greenling growth models generally indicated increased growth during warm conditions in the Alaska Coastal Current (17 significant coefficients), while in the California Current cool conditions in prior years (3 of 3 significant coefficients) and warm conditions in the current year were associated with faster growth (3 of 3 significant coefficients) (Table 3.2, Figure 3.3). For Kelp Greenling in the California Current, PDO and MEI during the prior year were negatively related to growth (PDO, $autumn_{L1}$; MEI for 2 consecutive seasons, $autumn_{L1}$-$winter_{L1}$), while conditions in the current year were positively related to growth (PDO in autumn and summer, MEI in autumn). For Kelp Greenling in the Alaska Coastal Current, growth was positively related to PDO with (7 consecutive seasons, $autumn_{L2}$-$spring_{L1}$) and without lags (2 consecutive seasons, spring-summer), negatively related to NPGO without a lag (4 consecutive seasons, autumn-summer), and positively related to MEI with (3 consecutive seasons $autumn_{L2}$-$spring_{L2}$) and without (summer) time lags.

Local-scale environmental variables were related to Black Rockfish and Kelp Greenling growth in both current systems (Table 3.3). Models of Black Rockfish growth improved with the addition of SST in 5 seasons ($spring_2$, $autumn_{L1}$, and 3 consecutive seasons winter-summer), SSHa in 8 seasons (4 consecutive seasons, $winter_{L2}$-$autumn_{L1}$; 2 consecutive seasons $spring_{L1}$-$summer_{L1}$, and 2 consecutive seasons spring-summer), upwelling in 6 seasons (2 consecutive

seasons, $winter_{L2}$-$spring_{L2}$; $autumn_{L1}$; $spring_{L1}$; and 2 consecutive seasons, autumn-winter), and PAR in 6 seasons ($spring_{L2}$, 3 consecutive seasons $winter_{L1}$-$summer_{L1}$; 2 consecutive seasons, spring-summer) (Table 3.3). Kelp Greenling growth models improved with the addition of SST in 7 seasons (5 consecutive seasons from $summer_{L2}$ to $summer_{L1}$ and 2 consecutive seasons from spring-summer), SSHa in 6 seasons ($autumn_{L2}$-$winter_{L2}$, $winter_{L1}$, $summer_{L1}$, winter, summer), upwelling in 6 seasons ($autumn_{L2}$-$winter_2$, $autumn_{L1}$, $summer_{L1}$, winter, summer), and PAR in 4 seasons ($spring_{L2}$-$summer_{L2}$, winter, summer) out of the 12 seasons examined (Table 3.3).

Black Rockfish growth in the California Current was inversely related to SST during 3 seasons ($spring_{L2}$, $autumn_{L1}$, and summer), inversely related to SSHa during 4 seasons ($winter_{L2}$-$summer_{L2}$ and $spring_{L1}$), positively related to SSHa during 2 seasons ($summer_{L1}$, spring), positively related to upwelling ($spring_{L2}$), inversely related to upwelling during 3 seasons ($spring_{L1}$, autumn-spring), and related to PAR during all spring seasons with positive relationships in $spring_{L2}$ and spring and a negative relationship in $spring_{L1}$ (Table 3.4, Figure 4.4). In the Alaska Coastal Current, Black Rockfish growth was positively related to SST in 4 seasons ($autumn_{L1}$, 3 consecutive seasons winter-summer) and positively related to upwelling in 3 seasons (2 consecutive seasons, $winter_{L2}$-$spring_{L2}$; $autumn_{L1}$). The SSHa and PAR had mixed relationships with rockfish growth (Table 3.4).

Model coefficients indicated that increased Kelp Greenling growth in the California Current was predominantly associated with cooler conditions, but an opposite relationship occurred in the summer of the current year (Table 3.4, Figure 3.4). Kelp Greenling growth was negatively related to SST ($summer_{L1}$), SSHa ($autumn_{L2}$-$winter_{L2}$, $summer_{L1}$, winter), and positively related to upwelling ($autumn_{L2}$-$winter_{L2}$, $summer_{L1}$, winter), and then positively related to both SST and SSHa in summer. Among Kelp Greenling captured in the Alaska Coastal Current, all coefficients indicated that warm conditions were associated with increased growth.

Growth was positively related to SST (6 seasons total in two groups; $summer_{L2}$-$spring_{L1}$ and spring-summer), SSHa (2 seasons, $autumn_{L2}$-$winter_{L2}$), upwelling (5 seasons; $autumn_{L2}$-$winter_{L2}$, $autumn_{L1}$, winter, summer), and PAR (4 seasons; $spring_{L2}$-$summer_{L2}$, winter, summer).

3.4 Discussion

We found that growth rates of Black Rockfish and Kelp Greenling in nearshore habitats of the California and Alaska Coastal Currents were related to basin- and local-scale indices of environmental conditions. In general, pelagic-feeding Black Rockfish grew faster during cool basin-scale conditions in the California Current and warm local-scale conditions in the Alaska Coastal Current. Benthic-feeding Kelp Greenling grew faster during and subsequent to warm basin- and local-scale conditions in the Alaska Coastal Current. In the California Current, Kelp Greenling growth response to climate was more complex, with both warm and cool conditions relating to increased growth at different time lags. Findings for pelagic-feeding Black Rockfish are consistent with perceived mechanisms for continental-shelf processes, whereas results for Kelp Greenling lead us to propose new hypotheses about processes involved in nearshore benthic production.

Otolith chronologies likely indicate biologically relevant species and ecosystem conditions. At the species level, otolith size correlates with somatic size (Campana 1990) and suggests that chronologies are related to interannual differences in somatic size and condition. In a recent study, Black et al. (2013) found that annual body mass indices (weight/length) of Yellowfin Sole (*Limanda aspera*) were well correlated with prior otolith growth at the population level. At the ecosystem level, rockfish otolith chronologies were synchronous with bivalve and tree-ring chronologies (Black 2009) as well as seabird reproductive success (Black et al. 2011), implying that otolith growth does reflect broad ecosystem conditions. Climatic events are particularly useful for identifying links between otoliths and biological responses at the species

and ecosystem levels. For example, the 1983 El Niño was associated with very narrow otolith growth increments (Black 2009), reduced levels of visceral fat (Lenarz and Wyllie Echeverria 1986), and recruitment failures (Lenarz et al. 1995) in rockfish as well as a general reduction of ecosystem production (Lenarz et al. 1995).

3.4.1 Black Rockfish, California Current

Basin and local-scale indicators correlated with growth of Black Rockfish in the California Current and generally suggest that cooler conditions were favorable for growth with and without time lags. Growth of California Current rockfish was related to PDO, NPGO, and MEI at the basin-scale and SST and SSHa at the local-scale. In the California Current, cooler climate conditions were previously linked to increases in pelagic production, including rockfish growth (Lenarz et al. 1995, Black 2009), rockfish condition (Lenarz and Wyllie Echeverria 1986), salmon catch (Hare et al. 1999), common murre (*Uria aalge*) reproductive success (Gladics et al. 2014), Cassin's Auklet (*Ptychoramphus aleuticus*) reproductive success (Sydeman et al. 2009; Wolf et al. 2009), forage fish abundance (Sydeman et al. 2013), zooplankton biomass and species composition (Peterson and Schwing 2003, Keister et al. 2011, Di Lorenzo et al. 2013), and chlorophyll-*a* concentrations (Harris et al. 2009; Boyce et al. 2010).

For Black Rockfish, cooler conditions may reflect increases in prey quality and abundance or favorable shifts in their prey composition or geographic distribution. Cooler conditions and less stable water columns associated with coastal upwelling indicate greater vertical mixing and nutrient availability to primary producers in the California Current (Chavez and Messié 2009, Demarcq 2009). Increasing nutrient availability causes bottom-up increases in phytoplankton and zooplankton abundance, and subsequent increases in forage fish consumption (Peterson and Schwing 2003, Harris et al. 2009, Boyce et al. 2010, Keister et al. 2011), condition (Astthorsson and Gislason 1998, Robards et al. 2002, Takahashi et al. 2012), and abundance (Hedd et al. 2006,

Thayer et al. 2008, Sydeman et al. 2013). Also, cooler conditions can prompt favorable shifts in prey composition (Hedd et al. 2006, Mackas et al. 2007, Thayer et al. 2008, Keister et al. 2011, Gladics et al. 2014). For example, during cool conditions Sand Lance and Northern Anchovy (*Engraulis mordax*) dominant seabird diets with commensurate increases in breeding success, while in warm years rockfish and Pacific Herring are more common in the diet and breeding success is lower (Hedd et al. 2006, Thayer et al. 2008, Gladics et al. 2014). Because Black Rockfish also consume these same forage fish species (Moulton 1977, Love 2011), increased availability of Sand Lance and anchovy may have similar benefits to their growth. Moreover, a shift to a forage fish community dominated by Sand Lance, which tend to be more closely associated with nearshore waters compared to other forage fish (e.g., herring) (Gladics et al. 2014), likely results in more spatial overlap of Black Rockfish with their prey.

Among local-scale relationships, there were also indications that warm conditions in the current year improved rockfish growth. Most of these relationships last only one season, suggesting the possibility of spurious relationships. Yet the pattern was evident in 3 indicators (SSHa, UW, and PAR), lending some credibility for cause and effect. Negative growth-upwelling relationships were particularly unexpected given previous established linkages between cool, nutrient rich surface waters and higher production (e.g., Barth et al. 2007; Chavez and Messié 2009; Black et al. 2011). The unexpected growth-upwelling relationship could be related to the development of nearshore fronts that prevent planktonic food resources from reaching nearshore food webs (Shanks and McCulloch 2003).

Seasons that were most informative for predicting Black Rockfish growth in the California Current were the winter and spring for basin conditions and spring for local conditions. Winter conditions might highlight the importance of preconditioning the water column for production (Polovina et al. 1995, Gargett 1997, Logerwell and Mantua 2003) or a winter upwelling mode

(Black et al. 2011). Spring conditions and the timing of the spring transition are known to be important for nutrient replenishment (Lynn et al. 2003), high levels of primary production (Hayward and Venrick 1998), and a sensitive phase for several marine animal populations in terms of recruitment, growth, and reproduction (Barth et al. 2007, Shanks and Roegner 2007).

3.4.2 Black Rockfish, Alaska Coastal Current

Local-scale indices are generally stronger predictors of Alaska Coastal Current rockfish growth than basin-scale indices. In the Gulf of Alaska, several studies indicate strong regional and local-scale variation in oceanography (Stabeno et al. 2004, Ladd et al. 2005), primary production (Waite and Mueter 2013), ichthyoplankton assemblages (Doyle et al. 2002), fish survival (Mueter et al. 2002), and fish growth rates (Hurst and Abookire 2006), suggesting that production may be more closely related to local-scale than basin-scale processes. Basin-scale climate-growth relationships were inconsistent in direction, and less persistent than local-scale relationships, indicating a higher likelihood of spurious relationships. Among local-scale indices, conditions that are associated with warm, more stable water columns were related to increases in fish growth (warmer SST, relaxed downwelling, increased PAR). Warm conditions in the Gulf of Alaska have previously been found to be associated with increases in salmon survival rates, salmon growth, and rockfish growth (Mueter et al. 2002, Wells et al. 2008, Black et al. 2008).

Black Rockfish results for the Alaska Coastal Current were consistent with a light-limited production system in the nearshore Gulf of Alaska pelagic food web (Gargett 1997, Brickley and Thomas 2004, Henson 2007), but do not necessarily rule out the possibility of nutrient-limitation. Light-limitation is thought to be common in the Gulf of Alaska as phytoplankton are adapted to high light conditions that are possible during long summer day lengths, but not necessarily common due to frequent cloud cover (Strom et al. 2010). In addition, spring blooms closely follow the onset of water column stratification (Henson 2007), which restricts phytoplankton to

the photic zone where light availability is greatest. Relaxed downwelling indicates both stabilization of the water column near the surface and the onshore movement of nutrient-rich water onto the Gulf of Alaska shelf at depth (Childers et al. 2005, Ladd et al. 2005, Weingartner et al. 2009). A recent examination of interannual variation in chlorophyll-*a* concentrations, a measure of phytoplankton standing stock and perhaps a metric of primary production, similarly suggested that increases in light (PAR) and relaxed downwelling improve pelagic primary production across the Gulf of Alaska shelf (Waite and Mueter 2013).

Just as in the California Current, increased primary production likely benefits Black Rockfish in the Alaska Current by increasing quality and quantity of their prey. Of the potential prey species, warm conditions have been associated with reductions in herring and greenlings and increases in Sand Lance and salmon (Anderson and Piatt 1999, Hare et al. 1999, Litzow et al. 2002). Sand Lance are one of the most energy dense nearshore forage fish species available to Black Rockfish and their abundance is strongly and positively related to interannual and spatial variation in summer SST in the nearshore Gulf of Alaska (Litzow et al. 2002). In a previous study, variation in Sand Lance growth was positively related to SST across years and primary production across sites (Robards et al. 2002). Thus, favorable influence of warmer temperature and increased primary production on Sand Lance abundance and condition may link local-scale conditions to Black Rockfish growth.

3.4.3 Kelp Greenling, California Current

Growth of Kelp Greenling in the California Current is related to basin- and local-scale indicators. Faster growth is associated with warm conditions with short or no time lags, but slower growth is associated with cool conditions with longer time lags. Among basin-scale indicators, this was the case for relationships with PDO and MEI (positive values of both represent warmer conditions). Similarly, warm local-scale conditions (warmer SST and increased SSHa) are

associated with increases in greenling growth without time lags and the cool conditions (cooler SST, reduced SSHa, and increased upwelling) are associated with a lagged increase in greenling growth. Few of these relationships are persistent across more than one season, but the consistent pattern across multiple indices suggested that relationships might be indicative of an underlying mechanism. Relationships between both cool or warm conditions and increased Kelp Greenling growth at different time lags could indicate that different conditions lead to more abundant prey versus higher quality prey.

Benthic invertebrates are important prey of Kelp Greenling (Moulton 1977, Rosenthal 1983) and previous work linking environment to benthic invertebrate production has led to both food- and temperature-limited production hypotheses. Support for food-limited recruitment (Menge et al. 2009) and growth (Menge et al. 1997, Bracken et al. 2012) in mussels has been suggested on the Oregon coast with cool upwelling conditions promoting increase in phytoplankton abundance that benefit benthic filter feeders. Indeed, the pelagic duration of many benthic larvae is short and confined to the productive upwelling season (Shanks and Eckert 2005), suggesting that high planktonic food availability is important for successful recruitment.

On the other hand, evidence of temperature-limited growth in benthic invertebrates has also been documented in the California Current, with faster mussel growth in warmer SSTs, despite reduced food availability near Point Conception (central California, USA) (Phillips 2005, 2007) and Santa Cruz Island (Channel Islands, California, USA) (Blanchette et al. 2006), and the Strait of Juan de Fuca (Strom 2004). Warm temperatures increase rates of filter feeding, providing a plausible mechanism linking temperature to growth increases (Phillips 2005). Both food availability and temperature were related to mussel growth rates in Oregon with direct thermal effects of temperature outweighing the indirect effect of food limitation, suggesting that

temperature limitations on food processing are more common than food limitation (Menge et al. 2008).

At the rocky reef study sites examined here the growth and condition of adult benthic invertebrates may not be food-limited by phytoplankton if kelp is the primary food resource (Duggins et al. 1989, Tallis 2009). Indeed, we found that kelp was the dominant carbon source for benthic Kelp Greenling and the presumed pathway for kelp-derived carbon is through their benthic invertebrate prey (Chapter 1). The complex growth response to environmental conditions observed here would be expected if recruitment of benthic invertebrates is phytoplankton-limited, while adult growth and reproduction are temperature-limited. Still, our understanding of benthic invertebrate production is based on information from only a few species of mussels, barnacles, and clams, which may or may not be representative of the benthic invertebrate community as a whole.

3.4.4 Kelp Greenling, Alaska Coastal Current

Basin- and local-scale relationships indicated that warmer conditions and more stable water columns (positive PDO, positive MEI, warm SST, increased SSHa, relaxed downwelling, and increased PAR) are associated with increases in Kelp Greenling growth. Negative current-year relationships between NPGO and growth are the exception to the positive relationship between temperature and growth. Relationships with PDO and SST were the most consistent predictors of growth. Environment-growth relationships were most common with 2 year lags or during the current summer of fish growth. Again, a mechanism involving Kelp Greenling prey may be responsible, as warmer conditions are associated with increased benthic invertebrate abundance (Blanchard et al. 2010), growth (Neuparth et al. 2002, Black et al. 2009, Stoner et al. 2010, Helser et al. 2012), development (Shirley et al. 1987, Hoegh-Guldberg and Pearse 1995), and reproduction (Hines 1982, Neuparth et al. 2002).

Warmer temperatures generally increase rates of growth, development, and reproduction of benthic invertebrates until thermal tolerance limits are reached or metabolic demands exceed food availability (Byrne 2011). For high latitude systems like the Gulf of Alaska, colder years are associated with prolonged larval durations, potentially resulting in increased mortality and cohort failure (Fisher 2006). By necessity, rocky nearshore benthic invertebrates are thermal generalists (Byrne 2011) and are more likely to respond positively to increased temperatures, because thermal tolerance is quite high. Therefore, we suggest that the positive relationship between temperature and Kelp Greenling growth may reflect increases in the abundance and quality of their benthic invertebrate prey during warmer conditions. Additional studies linking benthic invertebrate production to environmental conditions in the Alaska Coastal Current are needed to test this hypothesis.

3.4.5 Summary and conclusions

The results of this study are consistent with previous understanding of environmental influences on marine production and contributed to an improved understanding of how basin- and local-scale conditions may influence nearshore production in the future. Nearshore pelagic-feeding Black Rockfish generally benefit from cool conditions in the California Current and warm conditions in the Alaska Coastal Current in agreement with findings for continental shelf ecosystems that have been extensively studied. Basin-scale indicators were much better predictors in pelagic-feeding Black Rockfish in the California Current as compared to the Alaska Coastal Current, where local-scale indices were more informative. This pattern may indicate stronger or more coherent ties to basin-scale processes in the California Current and more local heterogeneity in the Alaska Coastal Current.

Findings for benthic-feeding Kelp Greenling were more nuanced and provided information for further hypothesis refinement and opportunities for hypothesis testing in future

studies. Mixed relationships between growth of benthic-feeding California Current Kelp Greenling and environmental conditions at different time lags may indicate that cooler conditions promote more benthic prey whereas warmer conditions promote increases in prey quality. The veracity of this hypothesis could reconcile long-disputed biophysical relationships in benthic production in the California Current that contrasts temperature (Phillips 2005, 2007, Blanchette et al. 2007) and food limitations (Menge et al. 1997, 2009, Menge and Menge 2013). Our hypotheses about various time lags and prey abundance and quality for benthic predators are testable.

Nearshore systems are particularly vulnerable to changing environmental conditions due to their shallow depths and location at the marine-terrestrial interface, which invokes variability from environmental drivers associated with both habitats (Agardy et al. 2005, Harley et al. 2006, Okey et al. 2014). Nearshore waters are expected to warm at rates up to twice as fast as offshore waters due to rapid warming of discharged freshwater (Okey et al. 2014), although eastern-boundary upwelling systems such as the California Current may experience cooler conditions due to strengthening of upwelling (Sydeman et al. 2014). Overall, the relationships between environmental conditions and nearshore production, indexed using otolith growth increments, generally agrees with the view that warming will have a negative influence at lower latitudes first, while production in higher latitudes may initially increase (Henson 2007, Boyce et al. 2010). Still, caution must be exercised when applying these relationships to future scenarios as unexpected patterns may arise given the non-stationary nature of climate-production relationships (Schmidt et al. 2014). Moreover, the food webs considered here are likely to be altered due to increasing storm frequency that diminish kelp forest canopies (Byrnes et al. 2011), increasing kelp production driven by rising CO_2 concentrations (Koch et al. 2013), increasing benthic invertebrate larvae mortality with ocean acidification (Byrne 2011), and changes in direct and indirect species

interactions with range shifts of individual fish species (Ainsworth et al. 2011), among other possibilities.

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Table 3.1. Model selection results for Black Rockfish and Kelp Greenling growth across systems using basin scale environmental indices (Pacific Decadal Oscillation, PDO; North Pacific Gyre Oscillation, NPGO; and Multivariate El Niño Southern Oscillation Index, MEI). Models in bold provided a better fit than models without the environmental variable as judged by AIC improvement of ≥ 2. The degrees of freedom and sample size (unique number of growth increments) were 13 and 3,134 for Black Rockfish models and 9 and 1,146 for Kelp Greenling models, respectively. Otolith growth increments spanned 1972-2010 for Black Rockfish and 1994-2010 for Kelp Greenling. *Alternative correlation structure was necessary for convergence of Black Rockfish models (see Methods).

Variable	Model	Black Rockfish ΔAIC	Kelp Greenling ΔAIC
None	Null	40.5	26.2
None	Null*	130.8	
PDO	$Autumn_{L2}$	42.7	**19.1**
	$Winter_{L2}$	**33.4**	**18.3**
	$Spring_{L2}$	**0.0**	**18.9**
	$Summer_{L2}$	**37.4**	**14.3**
	$Autumn_{L1}$	39.9	**5.0**
	$Winter_{L1}$*	**128.1**	**0.0**
	$Spring_{L1}$	43.9	**17.3**
	$Summer_{L1}$	44.5	24.4
	Autumn	41.8	**20.6**
	Winter	**38.5**	30.1
	Spring	41.1	**22.2**
	Summer	**31.7**	**0.5**
NPGO	$Autumn_{L2}$	**34.9**	25.7
	$Winter_{L2}$	**22.3**	24.9
	$Spring_{L2}$	**23.0**	25.7
	$Summer_{L2}$	**16.1**	24.6
	$Autumn_{L1}$	**28.7**	28.1
	$Winter_{L1}$	40.6	29.9
	$Spring_{L1}$	43.7	28.3
	$Summer_{L1}$	44.2	26.3
	Autumn	**34.7**	**14.1**
	Winter	**32.1**	**6.3**
	Spring	**38.2**	**15.9**
	Summer	40.8	**16.3**

Table 3.1 Continued…

Variable	Model	Black Rockfish ΔAIC	Kelp Greenling ΔAIC
MEI	$Autumn_{L2}$	38.8	**7.0**
	$Winter_{L2}$	**30.9**	**3.3**
	$Spring_{L2}$	**37.5**	**5.9**
	$Summer_{L2}$	44.1	24.6
	$Autumn_{L1}$	41.2	**18.2**
	$Winter_{L1}$	39.4	**17.4**
	$Spring_{L1}$	44.0	27.1
	$Summer_{L1}$	**22.3**	26.3
	Autumn	**6.2**	**20.7**
	Winter	**9.8**	24.8
	Spring	**28.0**	29.7
	Summer*	**107.9**	**20.5**

Table 3.2. Relationships between basin-scale climate indices (Pacific Decadal Oscillation, PDO; North Pacific Gyre Oscillation, NPGO; and Multivariate El Niño Southern Oscillation Index, MEI) and annual otolith growth increment width of Black Rockfish (1972-2010) and Kelp Greenling (1994-2010) from the California Current and Alaska Coastal Current across seasons (Autumn, Aut; Winter, Win; Spring, Spr; Summer, Sum) with lags of up to two years. Blank cells indicate non-significant relationships from mixed models. Effects were considered significant if the AIC value of the model decreased ≥2.0 compared to the same model without the basin-scale effect and the coefficient describing the effect was statistically significant ($P < 0.05$). The sign of the coefficient is noted in each box as either positive (Pos) or negative (Neg). Light and dark blue cells indicate relationships where cool conditions were related to increased fish growth at $P < 0.05$ and $P < 0.01$, respectively. Pink and red cells indicate relationships where warm conditions were related to increased fish growth at $P < 0.05$ and $P < 0.01$, respectively.

			2 years prior				1 year prior				Current year			
Species	Current system	Index	Aut_{L2}	Win_{L2}	Spr_{L2}	Sum_{L2}	Aut_{L1}	Win_{L1}	Spr_{L1}	Sum_{L1}	Aut	Win	Spr	Sum
Black Rockfish	California Current	PDO		Neg	Neg	Neg								Neg
		NPGO		Pos	Pos	Pos	Pos				Pos	Pos	Pos	
		MEI		Neg	Neg					Neg	Neg	Neg	Neg	Pos
	Alaska Coastal Current	PDO			Neg			Pos				Pos		
		NPGO	Pos	Pos		Pos	Pos							
		MEI										Neg		Pos
Kelp Greenling	California Current	PDO					Neg				Pos			Pos
		NPGO												
		MEI					Neg	Neg			Pos			
	Alaska Coastal Current	PDO	Pos	Pos	Pos	Pos	Pos	Pos	Pos				Pos	Pos
		NPGO									Neg	Neg	Neg	Neg
		MEI	Pos	Pos	Pos									Pos

$P < 0.05$	$P < 0.01$	Cool conditions related to increased growth
$P < 0.05$	$P < 0.01$	Warm conditions related to increased growth

Table 3.3. Model selection results for predicting Black Rockfish and Kelp Greenling growth using local scale environmental variables (sea surface temperature, SST; sea surface height anomalies, SSHa; upwelling, UW; and photosynthetically active radiation, PAR). Models in bold provided a better fit than models without the environmental variable as judged by AIC improvement of ≥ 2. The sample size (n) or unique number of growth increments are also reported for each model. Years in parentheses indicate the data record length of each environmental variable for comparison to Black Rockfish (1972-2010) and Kelp Greenling (1994-2010) growth increments. *Alternative correlation structure was necessary for convergence of Black Rockfish models (see Methods). Black Rockfish models have 13 degrees of freedom (12 degrees of freedom with the alternative correlation structure) and Kelp Greenling models have 9 degrees of freedom.

		Black Rockfish		Kelp Greenling	
Variable	Model	n	ΔAIC	n	ΔAIC
SST	Null	2914	22.5	1017	20.3
(1982-2010)	$Autumn_{L2}$	2914	26.0	1017	22.6
	$Winter_{L2}$	2914	21.3	1017	20.3
	$Spring_{L2}$	**2914**	**10.5**	**1017**	**20.7**
	$Summer_{L2}$	2914	25.7	**1017**	**16.7**
	$Autumn_{L1}$	**2914**	**8.5**	**1017**	**10.2**
	$Winter_{L1}$	2914	24.2	**1017**	**10.9**
	$Spring_{L1}$	2914	23.7	**1017**	**11.9**
	$Summer_{L1}$	2914	22.0	**1017**	**14.9**
	Autumn	2914	23.1	1017	23.9
	Winter	**2914**	**9.5**	1017	21.0
	Spring	**2914**	**19.5**	**1017**	**16.2**
	Summer	**2914**	**0.0**	**1017**	**0.0**
SSHa	Null	2611	11.2	1132	19.7
(1993-2010)	Null*	2611	43.6		
	$Autumn_{L2}$	2611	13.6	**1132**	**9.2**
	$Winter_{L2}$	**2611**	**5.1**	**1132**	**8.4**
	$Spring_{L2}$	**2611**	**4.2**	1132	23.5
	$Summer_{L2}$	**2611**	**5.2**	1132	20.8
	$Autumn_{L1}$*	**2611**	**33.3**	1132	23.7
	$Winter_{L1}$	2611	12.3	**1132**	**17.7**
	$Spring_{L1}$	**2611**	**0.0**	1132	18.0
	$Summer_{L1}$	**2611**	**6.3**	**1132**	**7.4**
	Autumn	2611	11.4	1132	22.7
	Winter	2611	14.6	**1132**	**15.0**
	Spring	**2611**	**4.2**	1132	22.8
	Summer	**2611**	**6.6**	**1132**	**0**

Table 3.3 Continued…

Variable	Model	Black Rockfish n	Black Rockfish ΔAIC	Kelp Greenling n	Kelp Greenling ΔAIC
Upwelling	Null	3134	17.4	1146	34.1
(1972-2010)	Null*	3134	107.7		
	$Autumn_{L2}$	3134	20.3	**1146**	**18.0**
	$Winter_{L2}$*	**3134**	**102.6**	**1146**	**19.3**
	$Spring_{L2}$*	**3134**	**70.8**	1146	37.5
	$Summer_{L2}$	3134	18.3	1146	37.6
	$Autumn_{L1}$*	**3134**	**104.5**	**1146**	**29.7**
	$Winter_{L1}$	3134	17.1	1146	36.9
	$Spring_{L1}$	**3134**	**10.4**	1146	33.3
	$Summer_{L1}$	3134	20.0	**1146**	**31.8**
	Autumn	**3134**	**0.0**	1146	34.0
	Winter	**3134**	**10.3**	**1146**	**0.0**
	Spring	3134	17.3	1146	33.8
	Summer	3134	20.4	**1146**	**20.2**
PAR	Null	2028	16.9	1044	24.7
(2000-2010)	$Winter_{L2}$	2028	15.6	1044	26.3
	$Spring_{L2}$	**2028**	**7.0**	**1044**	**6.0**
	$Summer_{L2}$	2028	19.9	**1044**	**0.0**
	$Winter_{L1}$	**2028**	**12.8**	1044	26.8
	$Spring_{L1}$	**2028**	**0.0**	1044	28.0
	$Summer_{L1}$	**2028**	**2.1**	1044	24.4
	Winter	2028	15.4	**1044**	**18.9**
	Spring	**2028**	**8.7**	1044	24.5
	Summer	**2028**	**11.5**	**1044**	**20.7**

Table 3.4. Relationships between local-scale climate indices (sea surface temperature, SST; sea surface height anomalies, SSHa; upwelling, UW; and photosynthetically active radiation, PAR) and annual otolith growth increment width of Black Rockfish and Kelp Greenling from the California Current and Alaska Coastal Current across seasons (Autumn, Aut; Winter, Win; Spring, Spr; Summer, Sum) with lags of up to two years. Blank cells indicate a non-significant relationship from mixed models. Effects were considered significant if the AIC value of the model decreased by ≥2.0 compared to the same model without the local-scale effect and the coefficient describing the effect was statistically significant ($P < 0.05$). The sign of the coefficient is noted in each box as either positive (Pos) or negative (Neg). Blue cells indicate relationships where cool conditions were related to increased fish growth and pink cells indicate relationships where warm conditions were related to increased fish growth.

			2 years prior				1 year prior				Current year			
Species	Current system	Index	Aut_{L2}	Win_{L2}	Spr_{L2}	Sum_{L2}	Aut_{L1}	Win_{L1}	Spr_{L1}	Sum_{L1}	Aut	Win	Spr	Sum
Black Rockfish	California Current	SST			Neg		Neg							Neg
		SSHa		Neg	Neg	Neg			Neg	Pos			Pos	
		UW			Pos				Neg		Neg	Neg		
		PAR			Pos				Neg				Pos	
	Alaska Coastal Current	SST					Pos					Pos	Pos	Pos
		SSHa					Pos		Neg	Neg				Pos
		UW		Pos	Pos		Pos							
		PAR			Pos			Neg	Pos	Pos				Pos
Kelp Greenling	California Current	SST								Neg				Pos
		SSHa	Neg	Neg						Neg		Neg		Pos
		UW	Pos	Pos						Pos		Pos		
		PAR												
	Alaska Coastal Current	SST				Pos	Pos	Pos	Pos				Pos	Pos
		SSHa	Pos	Pos										
		UW	Pos	Pos			Pos					Pos		Pos
		PAR			Pos	Pos						Pos		Pos

P < 0.05	P < 0.01	Cool conditions related to increased growth
P < 0.05	*P* <0.01	Warm conditions related to increased growth

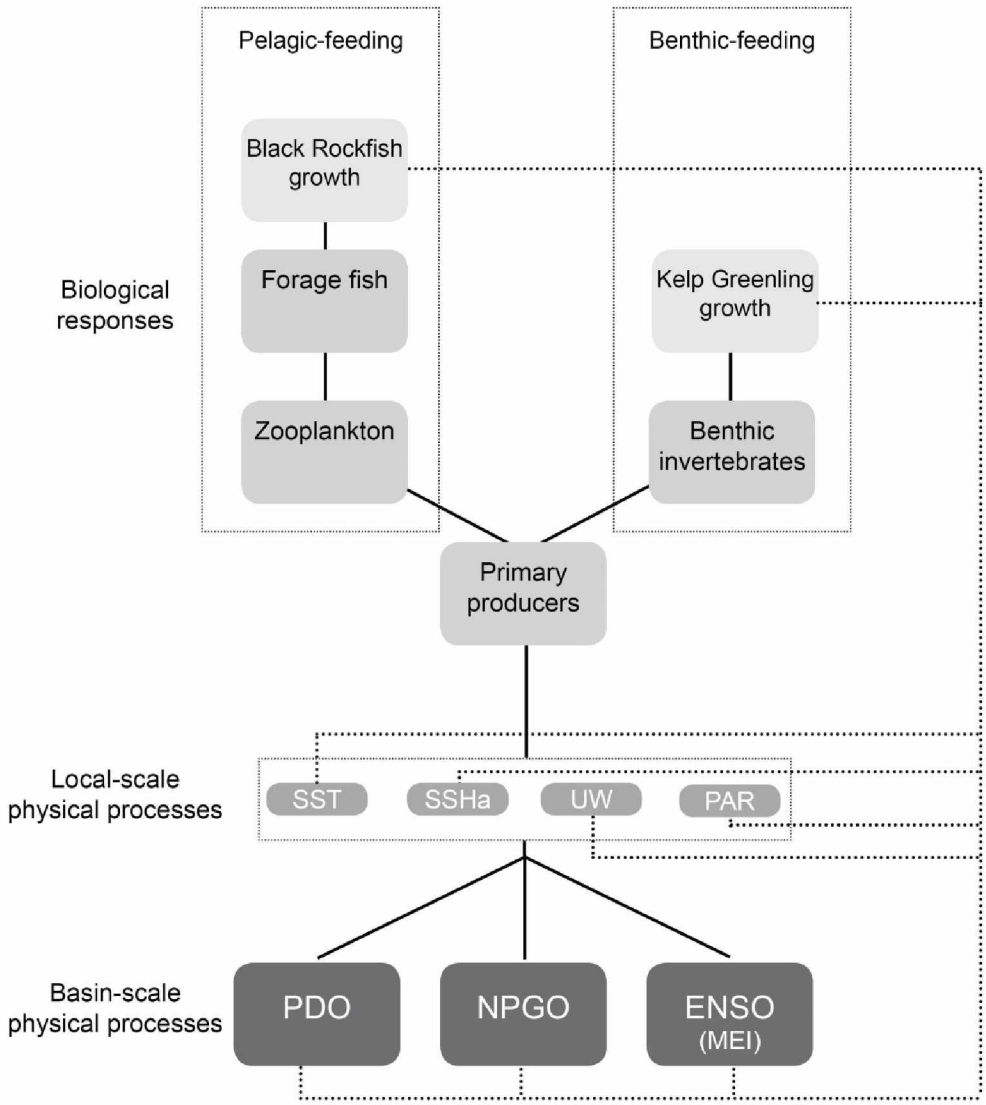

Figure 3.1. Conceptual diagram of food web responses to basin and local-scale processes. Basin-scale variables are represented by the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and the El Niño Southern Oscillation (ENSO), which is indexed by the Multivariate ENSO Index (MEI). Local scale processes are indicated by sea surface temperature (SST), sea surface height anomalies (SSHa), Bakun's upwelling index (UW), and photosynthetically active radiation (PAR). Solid lines represent conceptual relationships and dotted lines represent indirect relationships that were analyzed. Other relationships (e.g., direct effects of temperature on fish growth) were not included for simplicity.

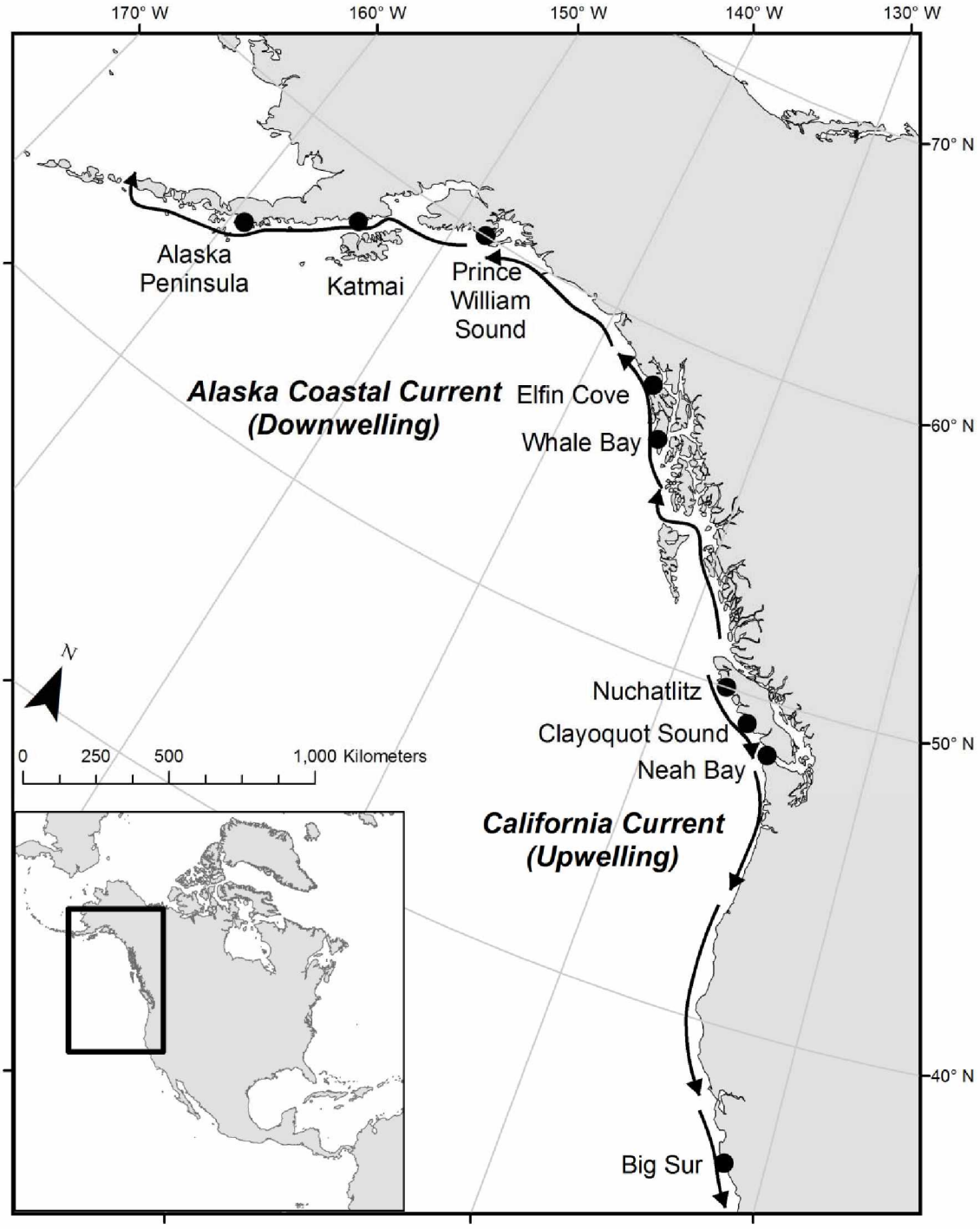

Figure 3.2. Nearshore fish collection sites (solid dots) and generalized nearshore current flow in summer (arrows) in the Alaska Coastal Current and California Current.

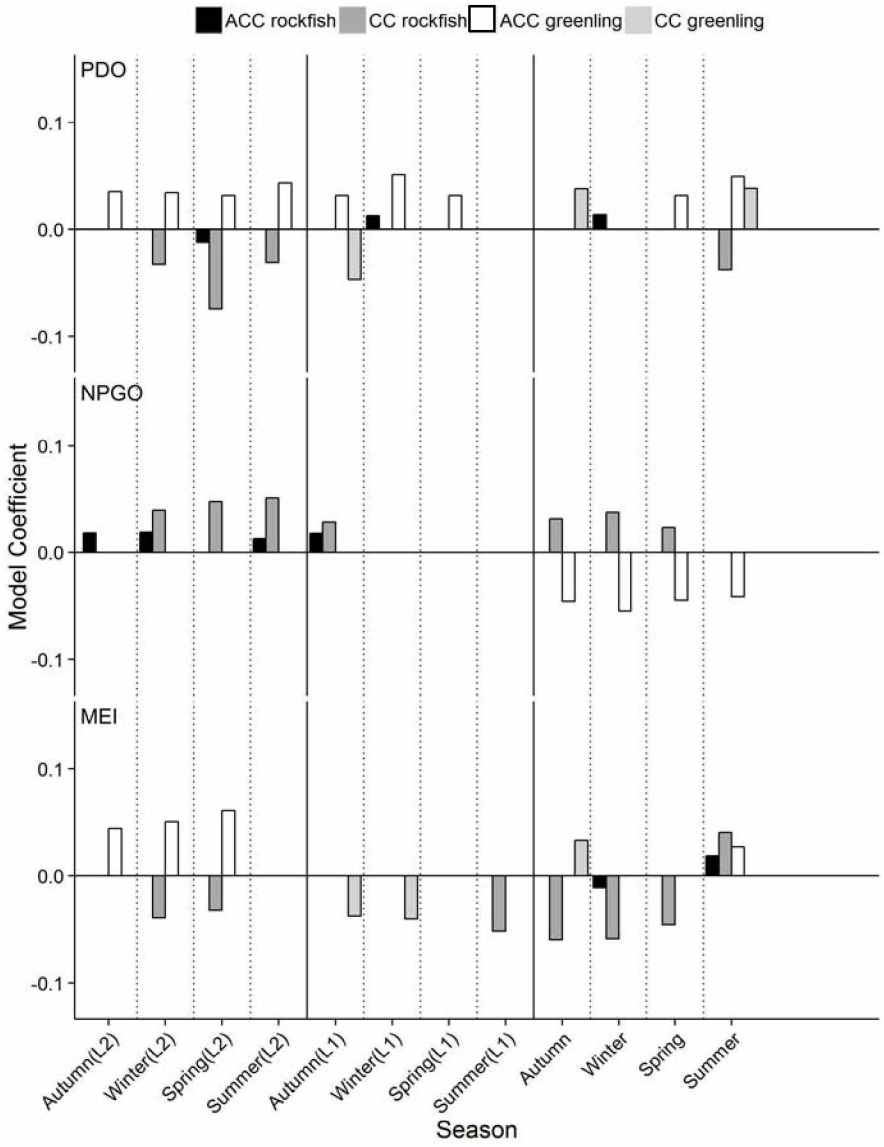

Figure 3.3. Model coefficients describing the relationship between annual otolith growth increments of Black Rockfish (1972-2010) and Kelp Greenling (1994-2010) and seasonal basin-scale environmental variables from mixed models with and without time lags. Basin-scale environmental variables include the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and the El Niño Southern Oscillation (ENSO) which is indexed by the Multivariate ENSO Index (MEI). Length of the annual lag is denoted in parentheses after the season name by a number following the letter L. Seasons were defined as autumn (Oct-Dec), winter (Jan-Mar), spring (Apr-Jun), and summer (Jul-Sep). Bar shading indicates the species and oceanographic current system: Black Rockfish from the Alaska Coastal Current (ACC rockfish), Black Rockfish from the California Current (CC rockfish), Kelp Greenling from the Alaska Coastal Current (ACC greenling), and Kelp Greenling from the California Current (CC greenling).

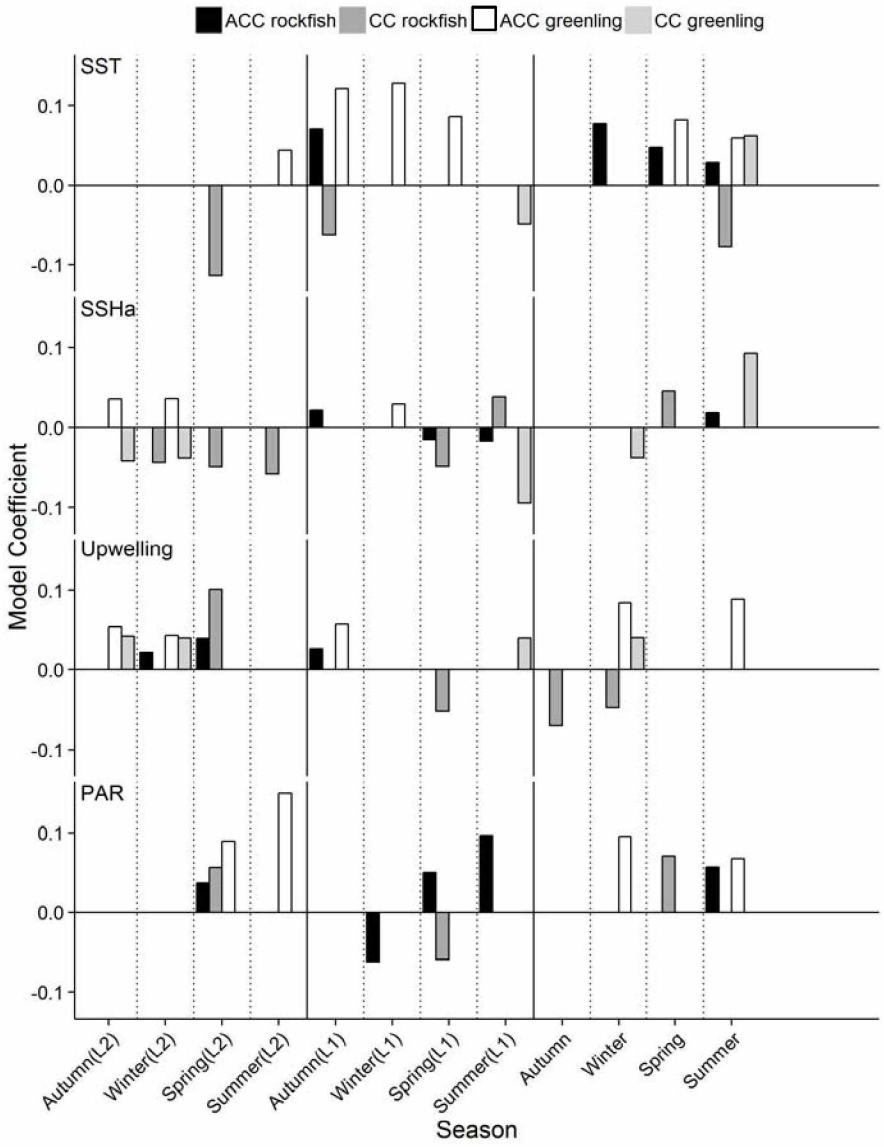

Figure 3.4. Model coefficients describing the relationship between annual otolith growth increments and seasonal local-scale environmental variables from mixed models with and without time lags. Local-scale indicators include sea surface temperature (SST), sea surface height anomalies (SSHa), Bakun's upwelling index (UW), and photosynthetically active radiation (PAR). Length of the annual lag is denoted in parentheses after the season name by a number following the letter L. Seasons were defined as autumn (Oct-Dec), winter (Jan-Mar), spring (Apr-Jun), and summer (Jul-Sep), except for PAR for which autumn measurements are unavailable and winter is only Feb-Mar. Bar color indicates the species and oceanographic current system: Black Rockfish from the Alaska Coastal Current (ACC rockfish), Black Rockfish from the California Current (CC rockfish), Kelp Greenling from the Alaska Coastal Current (ACC greenling), and Kelp Greenling from the California Current (CC greenling).

Conclusions

Understanding ecosystem structure and function can be extremely time consuming and costly, making examinations across multiple locations difficult and impractical. Natural indicators provide a feasible way to observe patterns *in situ* at multiple locations over ecologically relevant time scales (years to decades). In this dissertation, I used two types of natural indicators, stable isotopes and otolith macrostructure, to examine trophic structure and bottom-up biophysical relationships of two nearshore fish predators. Stable isotopes revealed that much of the carbon in pelagic and benthic feeding nearshore fish is derived from kelp primary producers, rather than just phytoplankton primary producers. Otolith macrostructure patterns were used to infer an annual growth record for individual fish and an indication of annual production that revealed several bottom-up correlates to fish growth and nearshore production.

In Chapter 1, stable isotope analysis revealed the widespread presence of kelp-derived carbon in benthic and pelagic-feeding fish across several locations in the northeast Pacific Ocean. To my knowledge, this is the first demonstration that kelp-derived carbon is a common source of primary production for nearshore fishes. The proportion of kelp-derived carbon was higher in Kelp Greenling than Black Rockfish, but kelp-derived carbon in both species was still substantial ($\geq$40%), suggesting that nearshore fishes could be dependent on kelp as a source of energy. Because the proportion of kelp-derived carbon was high for both benthic-feeding Kelp Greenling and pelagic-feeding Black Rockfish, these findings challenge the notion that kelp contributions are primarily restricted to benthic food webs though the direct consumption of grazing or capture of large pieces of detrital kelp (e.g., drift) by benthic invertebrates (Duggins et al. 1989). Instead, small pieces of detrital kelp may become suspended in the water column with

phytoplankton (Kaehler et al. 2006) and become widely available to benthic (e.g., mussels) and pelagic (e.g., zooplankton and forage fish) filter feeders that are subsequently consumed by fish, birds, and mammals (Foster and Schiel 1985). Our results support the hypothesis that stronger pelagic-benthic coupling occurs in nearshore systems, because predators can access both pelagic (e.g., phytoplankton) and benthic (e.g., kelp) energy channels (Kopp et al. 2015).

In Chapter 2, I tested several hypotheses relating environmental conditions in the summer to nearshore production using the annual otolith growth increments (i.e., otolith macrostructure) in nearshore fishes. Biophysical relationships differed between pelagic and benthic food webs, but these food webs included similar proportions of kelp- and phytoplankton-derived carbon, suggesting that differences in biophysical relationships do not arise from differences in primary production sources. My results were consistent with the notion that water column stability, indicated by sea surface temperature, regulates nearshore production in pelagic foods webs by controlling the availability of nutrients and retention of phytoplankton in the well-lit upper portion of the water column. Specifically, I found support for the Optimal Stability Window Hypothesis (Gargett 1997) that production in pelagic food webs was nutrient-limited in the California Current and light-limited in the Alaska Coastal Current. In benthic nearshore food webs, my results were consistent with the idea that temperature directly limits Kelp Greenling growth or the quality of benthic invertebrates, the main prey of benthic feeding fishes including Kelp Greenling examined here. In addition, growth of Kelp Greenling in the warmer California Current was consistently faster than in the cooler Alaska Coastal Current and may reflect a more productive benthic ecosystem in the California Current.

In Chapter 3, I expanded consideration of exploratory analyses involving basin-scale indices, other local-scale indices, all seasons, and included relationships with time lags to capture

whether changes in the environmental alter the quantity of prey using the same network of annual otolith growth increments developed for Chapter 2. The analyses in Chapter 3 were structured around the general expectation that cooler conditions improve production in California Current pelagic nearshore food webs and warmer conditions improve production in Alaska Coastal Current pelagic nearshore food webs and benthic food webs in both current systems. Lagged biophysical relationships were common and indicated the role of trophic interaction in bottom-up processes with the abundance of prey species influencing the growth of Black Rockfish and Kelp Greenling. Basin-scale climate oscillations were also related to fish growth, suggesting that nearshore production is responsive to large-scale conditions.

In general, pelagic-feeding Black Rockfish grew faster during cool basin-scale conditions in the California Current and warm local-scale conditions in the Alaska Coastal Current. Benthic-feeding Kelp Greenling grew faster during and subsequent to warm basin- and local-scale conditions in the Alaska Coastal Current. In the California Current, Kelp Greenling growth response to climate was more complex, and led me to propose new hypotheses about processes involved in nearshore benthic production. I suggested that cool conditions benefit recruitment of benthic invertebrates through increases in planktonic food availability and warm conditions benefit the growth and reproduction of adult benthic invertebrates through increases in temperature.

The analytical approach that I used in Chapters 2 and 3 to investigate the growth response of fish to abiotic conditions is unique in that it combined a crossdating technique from dendrochronology (Black et al. 2005) with a mixed model framework (Weisberg et al. 2010, Morrongiello et al. 2012). Crossdating was used to verify growth synchrony among individuals at each site and indirectly establish the accuracy of age assignments and growth increment

delineation. The mixed model framework offered maximum flexibility for the complex data set developed in this study, with fish collected from multiple study sites and each fish providing multiple, related, annual records in a hierarchical data structure. Moreover, it is well known that the width of an annual growth increment is related to a combination of intrinsic and extrinsic factors with the intrinsic factor of age having a much larger influence on the width of a growth increment relative to extrinsic environmental variables. Mixed models provide the opportunity to partition the variance among age and environment, while accounting for the hierarchical data structure and implementing an autoregressive correlation structure. In other words, I could structure the statistical models to match what I knew about the natural structure of the data and separate the influence of age from the environmental effect of interest.

Overall, this dissertation highlighted two important features of nearshore ecosystems: (1) Kelp energy is common in both pelagic and benthic food webs and (2) bottom-up limitations on production occur even in the most productive marine habitats. Management plans can now consider the trophic benefit of protecting and conserving kelp habitats for nearshore fishes and their marine birds and mammal predators. The evidence of bottom-up limitations in nearshore systems, combined with the observation that several commercially important fish species use nearshore system during early life history (Kruse and Tyler 1989, Dean et al. 2000, Laurel et al. 2007), suggests that nearshore production may influence the abundance of commercial species. Recruitment indices for nearshore rearing species should be compared to an index of nearshore production, such as otolith growth, to consider the possibility that interannual variation in nearshore production limits recruitment and survival. Ultimately, an index of nearshore production could be useful for managing nearshore rearing species such as Pacific Cod (*Gadus*

macrocephalus, Laurel et al. 2007), Northern Rock Sole (*Lepidopsetta polyxystra*, Hurst and Abookire 2006), or Walleye Pollock (*Theragra chalcogramma*, Sogard and Olla 1993).

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